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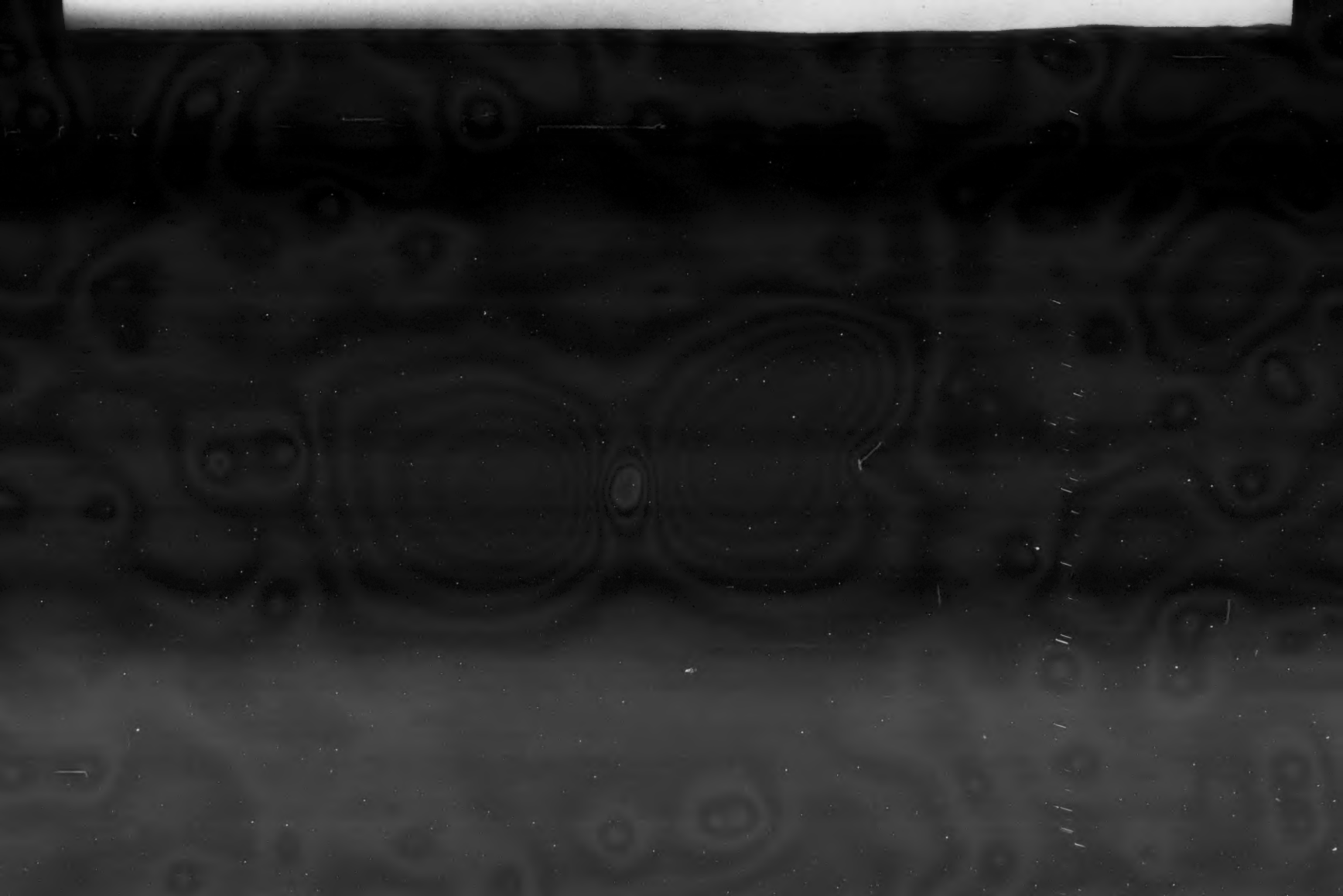

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THE
BOTANICAL GAZETTE

FEBRUARY 1911

THE ANATOMY OF THE SPORELING OF MARATTIA ALATA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 142

GRACE MIRIAM CHARLES

(WITH PLATES IX–XII AND THREE FIGURES)

The Marattiaceae combine to a unique degree the interest of an extremely ancient family with the significance of connections not only with other fern families but with the origin of seed plants. The recent discovery of the latter connection calls for more knowledge of the vascular anatomy of the living Marattiaceae, based upon abundant material.

Historical

The first studies of the anatomy of the Marattiaceae were based upon the mature stem of *Angiopteris evecta*. As the anatomy of this genus is the most complicated in the family, the first investigators, DE VRIES and HARTING (**7**), in 1853, concluded that the vascular system is composed of a tangled net of bundles running in every direction through the stem; and that the strands make a spiral of several cycles, which finally run out into the leaf traces. They made no distinction between leaf traces, stem bundles, and cortical roots.

In 1864 METTENIUS (**21**) investigated the stem of a large plant of *Angiopteris evecta* that had been languishing for eleven years before it was used for research. He considered that the vascular tissue is arranged in a series of concentric meshed zones or funnels, whose apex is at the base of the main axis of the stem and whose obliquely running bundles pass off from the periphery as leaf traces; that these leaf traces contain a definite number of bundles from

the peripheral zone, with the addition of two strands from the second zone; and that the gap in the second zone is repaired by a strand from the third, and so on through the four or five concentric zones that compose the stele. Toward the top of the broad stem the strands united into broad bands. METTENIUS thought that this might be due to the unhealthy state of the stem he used. In 1900 Miss SHOVE (**26**), reinvestigating a mature stem of *A. evecta*, confirmed his theory. She found a further difference in her material in the absence of strands from the second zone in the leaf traces. Otherwise her results confirmed those of METTENIUS.

In 1877 DE BARY (**6**) accepted METTENIUS' description of the mature stem of *A. evecta*, but found in the young stem a typical fern cylinder. In 1889 KÜHN (**17**) extended the work on juvenile forms to *Kaulfussia aeschylifolia* and *Marattia fraxinea*. Their steles consisted of a cylinder of bundles surrounding a central strand, which fused with the peripheral cylinder and went out as part of a leaf trace. He supposed that the place of the central strand was taken by a peripheral bundle bending in to the center. In the older plants of *Marattia*, instead of one there were two concentric series of bundles in whose center again was a medullary strand. In *Kaulfussia* the central strand was single, in *Marattia* it was made up of different strands at different levels.

Two important contributions to the knowledge of the anatomy of the Marattiaceae were made in 1902. (1) FARMER and HILL (**9**) investigated the young sporeling of *A. evecta*, filling in gaps in their material with *Marattia fraxinea* and *Kaulfussia aeschylifolia*. They found in the sporeling a single solid protostele which passed by a medullated stage to dictyostely or solenostely as the gaps are repaired. They found that the skeleton of *Marattia* is simpler than that of *Angiopteris*, because the leaves are not so crowded, although the leaf gaps are larger. (2) BREBNER (**3**) found that the sporeling of *Danaea alata* also starts with a protostele which does not pass through a medullated stage, but becomes crescentic after the departure of a variable number of leaf traces, and passes directly into the solenostelic stage. The medullary strand arises as a branch from the interior of the solenostele.

JEFFREY (**15**) in 1903 examined young stems of several species

of *Danaea* and one specimen of *Marattia fraxinea*, all of which had reached the stage of an amphiphloic siphonostele with a medullary strand. He found a tendency of internal phloeoterma to degenerate, and lists the Marattiaceae with pteridophytes that have developed endarch collateral bundles. He gives no description or figures of the stele in this stage.

It is evident that there is a fundamental difference in the transition from protostele to solenostele in *Angiopteris* and *Danaea*, that there are other important points in the various accounts that do not harmonize, and that *Marattia* has been examined only incidentally from a few specimens. It seemed desirable, therefore, to make a thorough study of a large number of sporelings of *Marattia* in all stages of development.

Material

A very generous supply of sporelings of *Marattia alata* of various ages was sent from Xalapa, Mexico, in November 1908 by Professor BARNES and Dr. LAND, who described to me the places in which the young sporelings were found. The most favorable locations were on the east slopes of the mountains near Xalapa, at an altitude of about 1140 meters, the temperature averaging about 30° C. The rainfall is 250 cm. per year, and although it is not evenly distributed, the moisture supply is sufficient to support a dense tropical rainy forest. In some places the upper vegetation had to be cut away to allow enough light to reach the ground to see the sporelings and prothallia. The most abundant supply of sporelings grew on the steep bank of a mountain torrent, in a soil composed of volcanic ash and yellow clay. Many of the youngest plants grew under the shelves made by the washing down of the surface; in one spot they grew just out of reach of the spray from a waterfall.

The prothallium may persist until the sporeling has five or six leaves, or the sporeling may become independent when its primary root is only a few millimeters long. The smallest sporeling, illustrated in fig. 4, had a primary root about 4 mm. long, and a cotyledon of the same length, whose blade was just forked. As the leaf grows older, the veins dichotomize further, and the cotyledon becomes spatulate. The first four or five leaves are of this type,

then unequal dichotomy of the middle vein sets in. Soon two lateral veinlets become prominent and form the midribs of two lateral lobes. This begins at about the 25th leaf. More pinnae are added in the same way until the pinnate adult leaf is established. The primary root is sparsely covered with coarse root hairs to within a millimeter of the tip. Hairs are less numerous on the secondary roots; and in the later roots the endophytic fungus also is less than in the primary root. The cortex of the stem, growing downward around the primary root, carries the first leaf traces down. Decay early attacks the primary root and works upward into the base of the stem. The secondary roots grow to a great length in proportion to the size of the plant, and seldom branch. In specimens 4 cm. long and 1 cm. in diameter roots extend a meter or more from the plant.

The sporelings examined ranged from the small one described to plants 2–5 cm. in diameter and 5 cm. long. Fig. 5 shows the tuberous form, the persistent swollen leaf bases (*l*) which with the stipules (*s*) hide the surface of the stem, the roots (*r*) that penetrate the old leaf bases, and the apex (*a*) inclosed by the interlocking stipules of the young leaves. The tendency to dorsiventrality shown by older *Angiopteris* stems does not appear in *Marattia;* the slight bend in a few specimens might easily be due to conditions of growth. The upper half of three of the larger plants elongated in proportion to the diameter, giving a flask-shaped contour to the plants. On the neck of the flask the leaves were separated by 0.5 cm. This change of habit from the bulky leaf-covered base was accompanied by an important simplification of the vascular anatomy that will be described later.

Methods

Part of the plants were killed when they were gathered, in a mixture of 50 per cent alcohol and 4 per cent formalin; part were sent to Chicago in damp moss and killed in the laboratory in chromacetic acid. They were imbedded in paraffin and the small sporelings cut 10 μ thick, the large ones 15–20 μ. A week or more in the oven at 52° was necessary to infiltrate the older stems. The stain best adapted for general differentiation of

vascular tissues was found to be the safranin-anilin blue combination. Early stages in the development of mucilage ducts came out better in Delafield's hematoxylon and safranin.

A clear conception of the course of the bundles can be gained rapidly by building up a clay model molded to match section by section. Though the proportions are not exact in this free-hand method, the relation of the bundles to each other is as accurate as in the wax models, and the saving of time is enormous.

Investigation

In the development of the stele of *Marattia alata* three stages stand out sharply: (1) the protostele; (2) the amphiphloic siphonostele, or solenostele; and (3) the polycyclic dictyostele. The transitions from one stage to the next, because they are rapid and varying, are the points about which wide differences of opinion center. Of the two transitions, that from the protostele to the solenostele is the most variable among ferns.

PROTOSTELE TO SOLENOSTELE

In the Schizeaceae (BOODLE **1**), the Cyatheaceae, and the Polypodiaceae (GWYNNE-VAUGHAN **11**), the first appearance of parenchyma in the protostele is at the periphery of the protostele at points just above the departure of leaf traces. The transformation works gradually inward. The internal parenchyma is therefore always in contact with the cortical parenchyma. In the *Lindsaya* type of stem and in *Matonia* (TANSLEY and LULHAM **27, 28**) internal phloem is differentiated within the xylem and comes in contact with the peripheral phloem at the leaf gaps. In *Pteris* (LECLERC DU SABLON **19**) a pith develops within the xylem.

In *Helminthostachys* (LANG **18**) the xylem, though sometimes solid, usually has parenchyma often conspicuous in the center, constituting a pith. Just below the origin of the first leaf trace the pith, if present, increases in size and is continuous with the parenchyma between the xylem of the leaf trace and that of the stele. If the stele is solid in the lower part of the internode, parenchyma appears in the center of the xylem in preparation for the departure of the leaf trace.

In *Angiopteris* (FARMER and HILL **9**) certain cell rows in the solid protostele cease to differentiate as tracheids, and form a pith which rapidly increases in importance, for the leaf traces soon involve the whole thickness of the xylem ring. As soon as gaps are left, the annular appearance is lost, peripheral phloem dips down and borders the pith, and then internal endodermis is differentiated as a late and secondary occurrence. In *Danaea* (BREBNER **3**) what appears to be pith separates the xylem of the outgoing leaf traces from the stele, and the stem passes at once from the protostelic to the dictyostelic condition.

In *Marattia* the protostele, usually solid at the cotyledonary node, may contain parenchyma cells, as in fig. 6. This is not definitely related to the center of the stele. When the first leaf trace goes off, a bay of the peripheral parenchyma may extend across the xylem. In this bay there may be isolated xylem elements which disappear later or join one or the other of the main xylem masses. The stele may become solid above and repeat the same process in giving off 4–9 more leaf traces, or it may contain scattered parenchyma from this time on. In the latter case the line of division for the next leaf trace is marked by the largest area of inclosed parenchyma. As in *Danaea*, a combination like the simultaneous departure of two or more leaves, or of a root and leaf, may give a temporary annular appearance (fig. 7), where the root trace (*rt*) is going off opposite the leaf trace (*lt*).

The stele may return to the solid protostele above such a cylindrical stage. The first leaf traces may take off half of the elements of the protostele. Later, the stele increases in size in proportion to the leaf traces, so that the line of division between stele and leaf trace cuts in a curve instead of straight across the stele (text fig. 1). Phloem and endodermis close in behind the leaf trace over the concave as over the plane surface of the protostele (fig. 8). Soon a leaf trace goes off from the side opposite the curve before it has rounded out (fig. 9). This leaves two segments of the stele separated by parenchyma (fig. 10). The diagrams (figs. 11–21) show the start of the next leaf trace, the penetration of phloem into the stele from the opposite side (figs. 13–15), its withdrawal as the strands close together (fig. 16);

also the repetition of this process for the next leaf, when the phloem closes around the xylem strands (fig. 17) and then disappears on the side where the former leaf went off (fig. 18). At the departure of leaf 3, endodermis as well as phloem penetrates between the two xylem strands (fig. 19), and in fig. 20 the cylinder with internal phloem and endodermis is established. The transition from protostele to solenostele with leaf gaps is represented in text fig. 1.

FIG. 1.—Diagram model of young stem in transition from protostele at the base to siphonostele at the top; the leaf traces leave constantly deeper crescents in the stele.

Angiopteris, *Danaea*, and *Marattia* agree more closely in structure than in interpretation of the tissues concerned in this transition from protostele to solenostele. The difference in interpretation involves the question whether the tissue not xylem within the endoderm is cortical or stelar. FARMER and HILL (**9**) are inclined to regard only vascular tissues as stelar. This leads to the difficulty of determining what tissues are vascular and what are cortical when there is no histological differentiation. At one level they regard a tissue as xylem parenchyma which in another closely related section they call pith (**9**, pl. 16, figs. 10, 11). The confusion caused by setting aside as non-vascular the pith in the Marattiaceae is the greater because of the widespread tendency to lignify only part of the xylem parenchyma. The primary as well as later roots may have a solid xylem core, or may be lignified only at the poles. The cotyledonary node, usually solid, may contain scattered parenchyma, and the bundles of the dictyostele have extensive bands of parenchyma (fig. 22). Another difficulty in the way of regarding this pith as non-vascular in the Marattiaceae is that the parenchyma is rarely definitely localized in the center of the stele, so that similar stages in the development of the stele of two plants of the same species would demand as different interpretations as those given to *Angiopteris* and *Danaea*. On the other hand, the parenchyma

that appears to separate the xylem of the outgoing leaf trace from the stele cannot be lightly dismissed, for the early appearance of this tissue related to more than one leaf is probably the origin of the pith in the Marattiaceae.

The obscurity of this transition is due to the telescoping of the dictyostelic into the protostelic stage. A slight extension of this process would result in the simultaneous origin of two or three leaves at the cotyledonary node, from which a dicotyledonous habit may have been derived in some offshoot of the family.

Rarely the solenostele forms a complete cylinder. It is generally broken by two or more leaf gaps, whose large size and close arrangement cause them to overlap. At this stage the bundle arrangement is like that in the Dicksonieae, some of the Polypodiaceae, and *Ophioglossum*. The last differs from the others in the collateral structure of the bundles. In some stems of *Marattia* the tendency toward a reduction of internal phloem and endodermis, referred to by JEFFREY (**15**), appears. This is not uniform, however, and is more likely to appear in the medium sized than in the larger stems.

THE MEDULLARY SYSTEM

When the stele reaches a diameter of 2–4 mm., a medullary strand appears and initiates the final stage in the development of the stele. It may originate in three different ways: (1) Most commonly it branches from the inner surface of the solenostele. Protophloem, otherwise absent on the inner surface of the stele, appears in a patch, which is bulged outward by an increase in parenchyma (fig. 23, *pph*), and later xylem elements increase at that point. Usually a root is given off from the external surface of the bundle opposite this branch (fig. 24). This is the origin described by FARMER and HILL (**9**) and BREBNER (**3**) as a "local hypertrophy of the internal phloem." (2) It may arise by a branch which runs into the pith from the upper part of the margin of a leaf gap. (3) The pith may develop a cambium which gives rise to a strand of phloem in the center of which xylem then forms. The xylem may run 0.3 mm. before a commissure connects it with the main vascular system.

The course of the medullary system is relatively uniform in different stems. The strand runs upward through the medulla toward a leaf gap that is about to close (fig. 25). It joins one of the margins of the gap, the strand on the other margin closes in, and the three strands form a plate of vascular tissue from whose outer surface a root usually goes off (fig. 25, *rt*). The medullary strand soon frees itself again while a leaf trace goes off from the vascular plate above the point where the medullary strand joined the main vascular system. Farther on in its course the medullary strand sends a short branch into the main system, and this is not given off again but goes out with a leaf trace (fig. 25, *ms*). As the leaf traces become more crowded (text fig. 2*a*) the medullary strand divides into a greater number of parts, which join the main system at the closing of the leaf gaps. Occasionally a gap closes without a strand from the medullary system. At this stage *Kaulfussia* (**17**) and *Archangiopteris* (**12**) closely resemble *Marattia*.

FIG. 2*a*.—Exterior view of diagram model of the stele at the stage when the medullary strand appears; the medullary strands can be seen through the upper leaf gap.

Further complications of the medullary system of *Marattia* come from combinations of anastomoses and branching (text fig. 3). In *Matonia* the second cylinder is developed from the solid central strand

in the same way that the protostele in it becomes a siphonostele, by the differentiation of a strand of phloem in the center of the xylem. This repetition of the process by which the first cylinder was made does not take place in *Marattia*, but the medullary system becomes cylindrical by the anastomosis of two central strands (text fig. 3) in one case, although there are suggestions that the cylinder may also be formed by the branching of the strand as KÜHN (**15**) suggests. In the one clear case of the formation of the second cylinder in my material two medullary strands fuse to form a crescent. A branch from one horn of the crescent passes over to the other horn, then a strand from the first horn is cut off and runs out to a leaf gap. Further branching breaks up the secondary solenostele.

FIG. 2*b*.—The same as fig. 2*a*, with the side cut away to show the course of the medullary strand.

On account of the spiral arrangement of the leaves, the medullary strand that shares in closing a leaf gap at one level makes part of the vascular tissue of the leaf above in that rank. When the crowding of the leaves breaks the regularity of the spiral the medullary strand is less definitely related to the leaf traces. The influence of the compact form of the stem is further emphasized in the stems described above whose upper half elongates. In these the medullary strand

branches less and less frequently, until it finally joins the main vascular system and is not given off again (fig. 25). At the same time the strands of the main vascular system unite into a solenostele with a single leaf gap. This is the same sort of behavior as that in the plant examined by METTENIUS (**21**). The compact habit of *Marattia* is therefore responsible for two of its most striking differences from the Psaroniae (**22**): the shape of the bundles, which are band-shaped in *Psaronius* and elliptical in *Marattia;* and the relation of the medullary system to the leaf traces.

The relation of the roots to the external and to the medullary systems differs in the mature stem examined by Miss SHOVE (**26**) and in the young stems of *Marattia*. In the latter the main root supply joins the external system, while the medullary system has a few small roots. In *Angiopteris* the largest number of roots is attached to the internal system. This difference may be due to the greater importance of the internal system in the older stem, or to the possibility that the meshes that apparently belong to the external system in the mature stem really belong to the leaf traces, and the second zone is homologous with the main vascular system to the young stem.

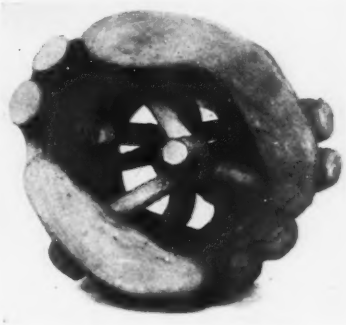

FIG. 2*c*.—Upper end view of fig. 2*a*.

In comparing the medullary systems of *Marattia* and the solenostelic ferns described by GWYNNE-VAUGHAN, some important differences appear. In the latter the origin of the system is the elaboration of a thickened leaf gap margin. The thickening works upward and downward, and in *Alsophila* (**11**) the strands are decurrent into the pith. In *Marattia alata* the origin is from an internal branch above a leaf gap, from the top of a leaf gap, or from a cambium in the medulla. In the solenostelic ferns the connections of the medullary with the main vascular system are generally at the nodes and along the leaf gap margin, although in *Pteris elata*

it connects at the anterior end of the leaf gap. In *M. alata* it joins the external system in the internodes, is freest at the nodes, and is concerned with the closing of the leaf gap. In the solenostelic ferns roots are not connected with the internal system as they are in the Marattiaceae. In such solenostelic ferns as have more than one concentric cylinder in the medullary system, as in *Matonia*, the

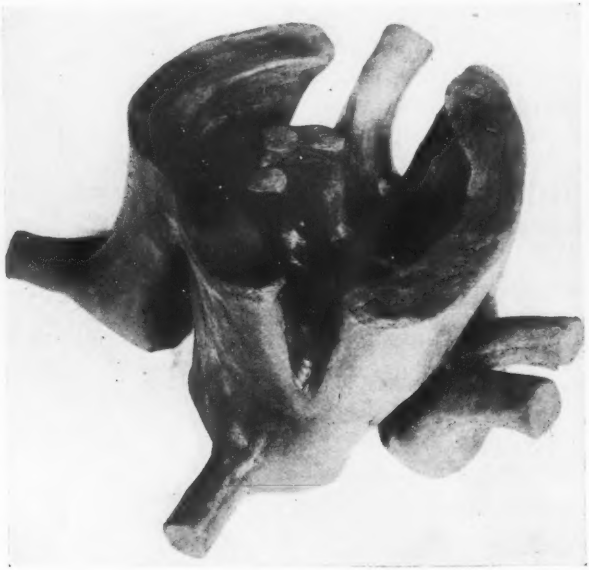

FIG. 3.—View from the upper side of a model, showing the origin of a medullary cylinder from the anastomosis and branching of two medullary strands.

formation of the second cylinder is markedly different from that in *Marattia*. In the Cyatheaceae the medullary strand takes part in the formation of several leaf traces, in *Matonia* it is a definite part of a single trace. In *Marattia* it shares in forming the region from which a leaf trace goes off.

If the medullary system of Marattiaceae is homologous with that of the Dicksonieae, Cyatheaceae, and Polypodiaceae, modifications must have taken place in the Marattiaceae. The place of

origin must have shifted upward and sidewise, so as to come above a leaf trace instead of along the margin of the gap left by it, as has taken place in *Alsophila*. The later connections must have made the same change in relative position of internal and external systems. In view of the wide distribution of medullary strands in remote groups of the pteridophytes, however, it is not certain that they are homologous even in these closely related families.

A comparison of the young stem of *Marattia* with that of *Psaronius* shows some points of resemblance more sharply than appear in the mature vascular system. The band-shaped bundles, the close relation of the medullary system to the leaf traces, and the simple leaf traces are alike in the young *Marattia* stem and in *Psaronius*. The absence of roots on the medullary system of *Psaronius* may be due to the relatively small gaps in the peripheral cylinder. The slight relation of the peripheral bundles to the leaf traces may be due, as RUDOLPH (**21**) has suggested, to the ranked or simple spiral arrangement of the leaves. It may be that the tendency to free origin and ending of medullary strands in *Marattia* indicates a reduction from the high state of development of such strands in *Psaronius*, as such similar free endings have been interpreted in the petioles of *Ceratozamia* (DORETY **8**) and *Botrychium* (CHRYSLER **5**).

PROTOXYLEM

The variability of protoxylem noted by GWYNNE-VAUGHAN (**11**) and TANSLEY (**28**) in Filicales generally reaches a high expression in *Marattia alata*. The first xylem elements to develop appear at the cotyledonary node. They may be the slender spiral tracheids common in ferns, similar small vessels with reticulate thickenings, as in *Dicksonia apiifolia*, or stretched scalariform vessels of the same caliber as the other elements of the xylem strand; or there may be no distinction between the first vessels and those developing later as in *Angiopteris* (FARMER and HILL **9**) and *Danaea* (BREBNER **3**). In the last case the change to the primary root is brought about by a reduction in the xylem at opposite sides of the bundle, development of protoxylem at the ends of the xylem band, and disappearance of phloem at the ends and increase at the sides of the xylem. In two primary roots there were three poles instead

of the two that prevail generally. As the pericycle is delicate and irregular, the protoxylem of the root often abuts on the endodermis.

In a few specimens spiral exarch protoxylem is present in the cotyledonary node. This is continuous with the protoxylem at the poles of the primary root and in the first leaf trace. In other stems the mesarch position characteristic of the older stem appears at the cotyledonary node. The same unsettled condition persists in the solenostele, although an examination of the apical region shows that the first elements lignified are toward the center of the stem. In the strands of the dictyostele definite protoxylem points appear in an endarch position, with occasionally one or two centripetal elements beyond them (fig. 22). These bundles do not show the distinction between large bundles with mesarch or no protoxylem, and small strands with endarch protoxylem observed in *Angiopteris*.

The cotyledonary trace shows the same kind of variations in the position of the protoxylem as the cotyledonary node. It may be exarch where it joins the stele (fig. 26) and gradually shift to mesarch (figs. 26–30) in the petiole; no protoxylem may be distinguishable in the trace near the stele, but a development of it in a mesarch position occurs while the trace is passing through the cortex; or the trace may consist of only two or three scattered elements. The next three or four leaves are mesarch, and may become endarch in the upper part of their course. The older leaf traces are endarch as in *Angiopteris* and *Danaea*.

APICAL MERISTEMS

The apical regions of *Marattia* have been the source of much difference of opinion. HOFMEISTER (**13**) described a single deep triangular apical cell for the Marattiaceae, as for all other vascular cryptogams. According to HOLLE (**14**) a four-sided apical cell is found in the stem of the young sporophyte and is retained permanently. BOWER (**2**) describes for mature plants a 4 or 5-celled meristem meeting at the intersection of two more or less perpendicular lines. CAMPBELL (**4**) found that in some cases at least the apex of the stem is occupied by a single initial. FARMER and HILL (**9**) describe an apical cell of irregular prismatic form,

though sometimes triangular in cross-section, in the apex of the young stem of *Angiopteris*, and BREBNER (**3**) concluded that *Danaea* was the same.

Such differences of opinion show that there is either variation or vagueness in the structure observed. In this case both enter into the result. In very young stems there is a triangular pyramidal apical cell (fig. 31). This soon becomes prismatic, and the outline of the triangle in cross-section becomes irregular (fig. 32). Gradually it becomes four-sided (fig. 33). Then one of the latest segments begins to act as an apical cell, and there are two blocks of meristematic cells at the apex (fig. 34). In longitudinal view two sections separated from each other show two large vacuolate cells cutting off segments from the base. The division of the segments is very irregular. In a still larger stem the apex was occupied by a meristem (fig. 35).

The growing point of the young stem is close to the base of the youngest leaf and very narrow (fig. 36). As the stem grows older the apex grows broader. At the solenostelic stage the tissue below the center of the apical cell is large-celled pith (fig. 37).

The root apex has received more attention than that of the stem. The three-sided cell, probably derived from the octant of the embryo, has been observed in *Angiopteris*. A similar cell occurs in the apex of the very young primary root of *Marattia*. As in the stem, a four-sided prism soon appears, which HOLLE (**14**) thought was permanent. SCHWENDENER (**25**) held that it divided into four about the axis of the root, and BOWER (**2**) agreed with him. RUSSOW (**23**) found a group of initials. KOCH'S (**16**) explanation for the different situations that occur is ingenious. The evidence, however, of a regular sequence of divisions and fan-shaped growth of one segment with consequent shifting to the center is not entirely convincing. A possible explanation is that there is no fixed structure or behavior in the apex of the root.

New roots originate in the meristematic region of the stem before differentiation of tissue has begun. FARMER and HILL (**9**) maintain that the origin is a single six-sided prismatic cell of the endodermis cutting on the sides and ends. According to DE BARY (**6**)

root origin in pteridophytes, with the exception of Lycopodiales, is endodermal, as contrasted with the prevailing pericyclic root origin in seed plants. In *Marattia* the pericycle is not a true pericycle, since it is composed of sister cells of the endodermis, and the phloem may abut on the endodermis. Roots originate within the undifferentiated cylinder (fig. 38). Periclinal divisions work outward and laterally (fig. 39) and into the cortex which forms the periblem of the young root (figs. 40, 41).

The chief work on apical regions was done under the influence of HANSTEIN'S theory of a rigid morphological distinction between periblem, plerome, and dermatogen. SCHOUTE (**24**) has shown that the apical divisions do not determine the limits of the tissues developed from them. This leads to the view that the character of the apical region is determined by the bulk of the organ and has no other significance. Whether the transition from the fernlike apical cell to a meristematic region has any phylogenetic significance, must be determined by finding whether other bulky plants show this variability. Some species of *Selaginella* have more than one apical cell (RUSSOW **23**), but with this exception *Marattia* is unique in this character.

MUCILAGE DUCTS

Soon after the solenostelic stage is established, a mucilage duct may appear in the center of the pith. A branch from it runs out along the adaxial side of each leaf trace, and branches and anastomoses in the cortex of the stem and petiole. FARMER and HILL (**9**) follow KÜHN (**19**) in ascribing a lysigenous origin to these ducts. BREBNER (**3**) holds to the schizogenous origin in *Danaea* at the upper ends of the ducts. *Marattia* resembles *Danaea* in the division of the parenchyma cell into four to six without increase in size, and the separation of the walls where the small cells come together. The contents of the small cells stain deeply with anilin blue, and the nuclei, gathered around the point where the cells are to break apart, are small and denser than the nuclei in the surrounding parenchyma cells. The space left when the walls break apart appears empty at first, then becomes filled with a vacuolate substance that stains with anilin blue. Later the reaction of this

mucilage to stain changes rapidly and it takes the safranin. At this time and earlier than in *Danaea* the small cells begin to break down and the mucilage becomes stringy (fig. 41). The small cells do not break down uniformly; they may extend into the cavity of the duct as the "bridge-cells" of *Danaea* or float in the mucilage. The schizogenous stage may be omitted and cells of the pith break down into mucilage directly. Although tannin cells are numerous, none appeared to be changing to mucilage ducts as LUTZ (**20**) describes for *Angiopteris*. The origin and development of the mucilage ducts in the seedling of *Microcycas* are identical with those of *M. alata*.

Summary and conclusions

1. The transition from protostele to solenostele in *Marattia* is sudden and without the intervention of a definite medullated monostelic stage. The indefinite hints of pith due to the early start of parenchyma to divide leaf trace from stele may be the origin of the medullated stage.

2. The medullary system of *Marattia* differs from that of the solenostelic ferns in origin, course of bundles, and development into a cylinder. It resembles that of *Psaronius* in its relation to leaf traces.

3. Elongation of the stem causes the union of the bundles into broad bands and a reduction of the medullary system. This emphasizes the close relation between the compact habit and crowded leaves of *Marattia* and the number of concentric cycles and leaf gaps in the dictyostele. The difference in habit, therefore, accounts for the difference in the anatomy of *Marattia* and the more elongated Marattiaceae, *Danaea*, and *Kaulfussia*, and the treelike *Psaronius*.

4. The occurrence and position of protoxylem varies. It may not be distinguishable or may consist of spiral or modified reticulate tracheids. When distinguishable, it may be in an exarch or mesarch position in the cotyledonary node, mesarch in the protostele above the cotyledonary node, and usually endarch in the strands of the older parts of the stem. Similar variations occur in the leaf traces. The cotyledonary trace may change from

exarch to mesarch, the later leaves from mesarch to endarch. Mature leaf traces are endarch.

5. Apical meristems vary from the fernlike triangular apical cells in young sporelings to meristematic groups in older stems and roots. Such variation during the course of development occurs in the gametophytes of pteridophytes and in some liverworts, but is not recorded for the sporophyte of other ferns.

6. The cotyledonary trace is collateral during most of its course. Later leaf traces start collateral and develop adaxial sieve tubes in their course through the cortex. Some stems show a slight tendency toward a reduction of internal phloem and endodermis, others an increase in the older part of the stem. The basis for classifying the Marattiaceae with pteridophytes that have developed collateral bundles is therefore insecure.

7. Secondary roots originate from vascular tissue before differentiation into regions has begun. The cortex shares in forming the cortex of the root.

8. Mucilage ducts originate both schizogenously and lysigenously, generally the former.

Marked instability is characteristic of *Marattia*. The Ophioglossaceae share this trait in root structure, the Dicksonieae in protoxylem position. Only gametophytes have such a transition of apical regions. Combined with variability is the indefiniteness of the medullated monostelic stage. Such instability is characteristic of plants that give rise to new lines. It is evident that the Marattiaceae have retained many characters of the stock from which branched off the Ophioglossaceae, then the Psaronieae and Cyatheaceae. It is probable that the compact habit of the Marattiaceae was developed after the lines connecting with the other families had diverged, since the characteristics due to it are also unstable.

This investigation was carried on at the University of Chicago, under the direction of Professor JOHN M. COULTER and Dr. W. J. G. LAND, to whom I wish to express my thanks for criticism and advice.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES IX–XII

With the exception of figs. 4, 5, 11–21, and 25, all drawings were made with the aid of an Abbé camera lucida and reduced one-half in reproduction. Abbreviations are as follows: *c*, cotyledon; *en*, endodermis; *l*, leaf; *lb*, leaf base; *lt*, leaf trace; *ms*, medullary strand; *pa*, parenchyma; *ph*, phloem; *pph*, protophloem; *pr*, prothallium; *px*, protoxylem; *r*, root; *rt*, root trace; *s*, sieve tube; *st*, stipule; *x*, xylem.

FIG. 4.—Young sporeling attached to the prothallium, with the second leaf appearing. ×2.5.

FIG. 5.—Older sporeling, showing persistent leaf bases (*lb*). ×1.

FIG. 6.—Transverse section through the cotelydonary node, showing parenchyma cells among the xylem. ×400.

FIG. 7.—Transverse section through the stele, showing apparent pith due to the simultaneous departure of the root trace (*rt*) and leaf trace (*lt*) opposite each other. ×188.

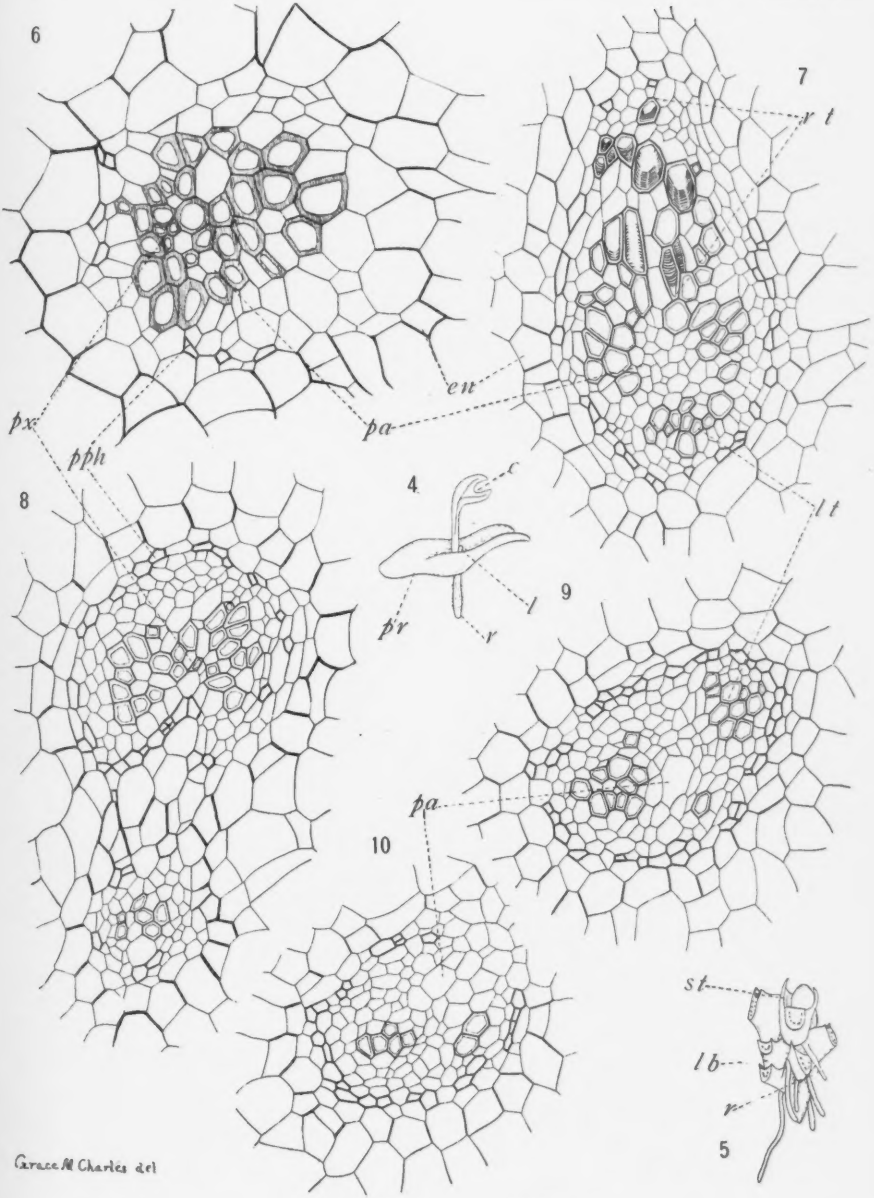
FIG. 8.—Transverse section of the same 50 μ above fig. 7, showing phloem (*ph*) and endodermis (*en*) cutting in a curve behind a leaf trace. ×188.

FIG. 9.—Transverse section of the same 40 μ above fig. 8, showing the departure of the next leaf trace (*lt*) and a persistent cell of cortical parenchyma (*pa*). ×188.

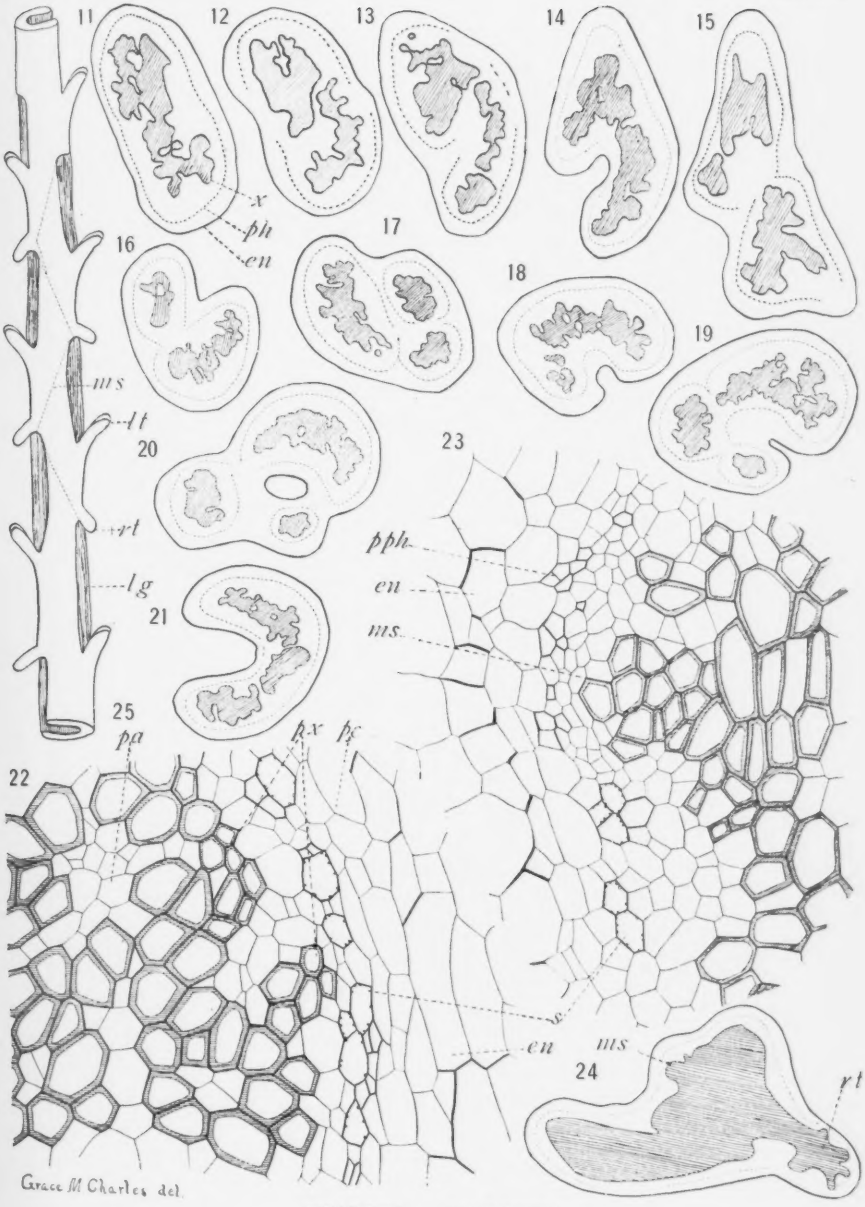
FIG. 10.—Transverse section of the same 40 μ above fig. 9, showing cortical parenchyma (*pa*) at the side of the stele, contrasting with xylem parenchyma in size. ×188.

FIGS. 11–21.—Diagrams of successive stages in the transition from protostele to solenostele.

FIG. 22.—Transverse section from the inner surface of a dictyostelic bundle, showing endarch protoxylem, bands of parenchyma, sieve tubes, pericycle, and endodermis. ×188.



CHARLES on MARATTIA



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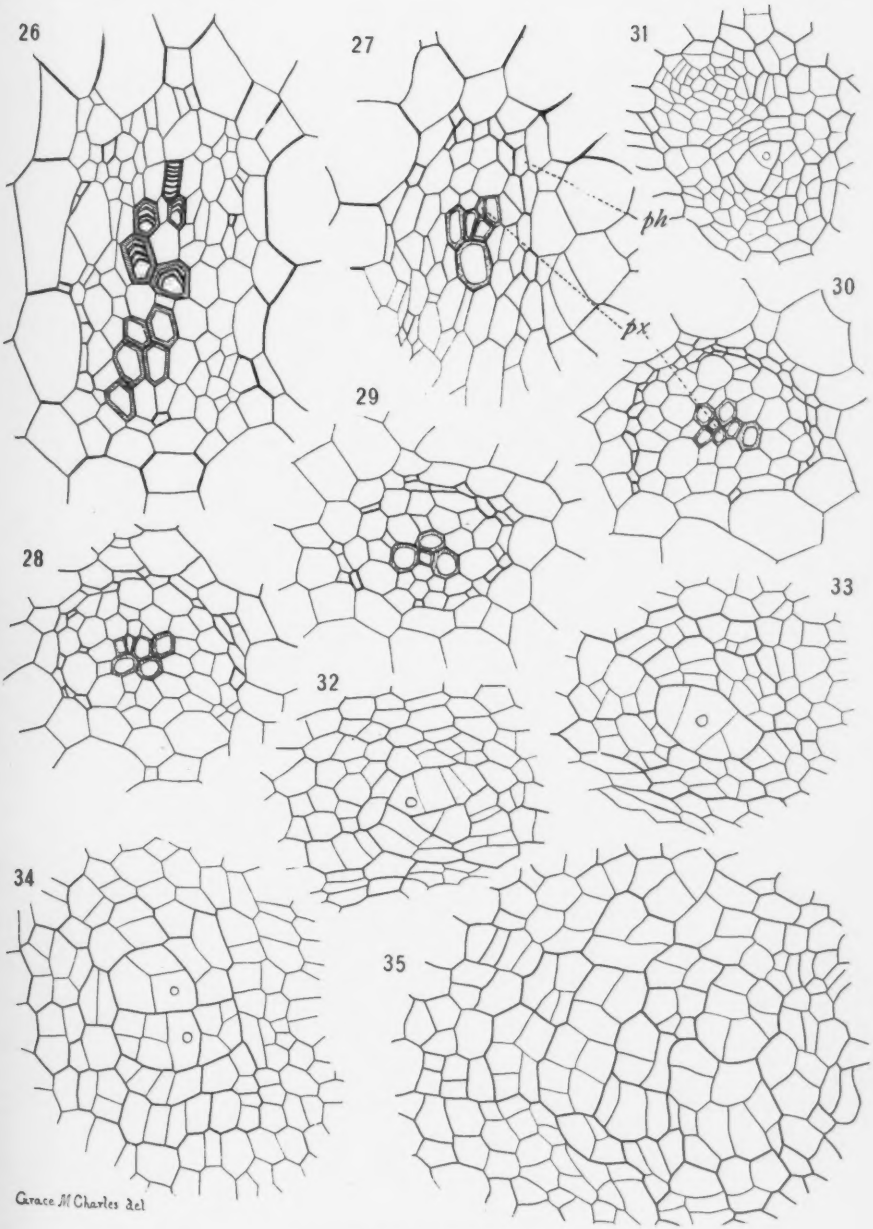

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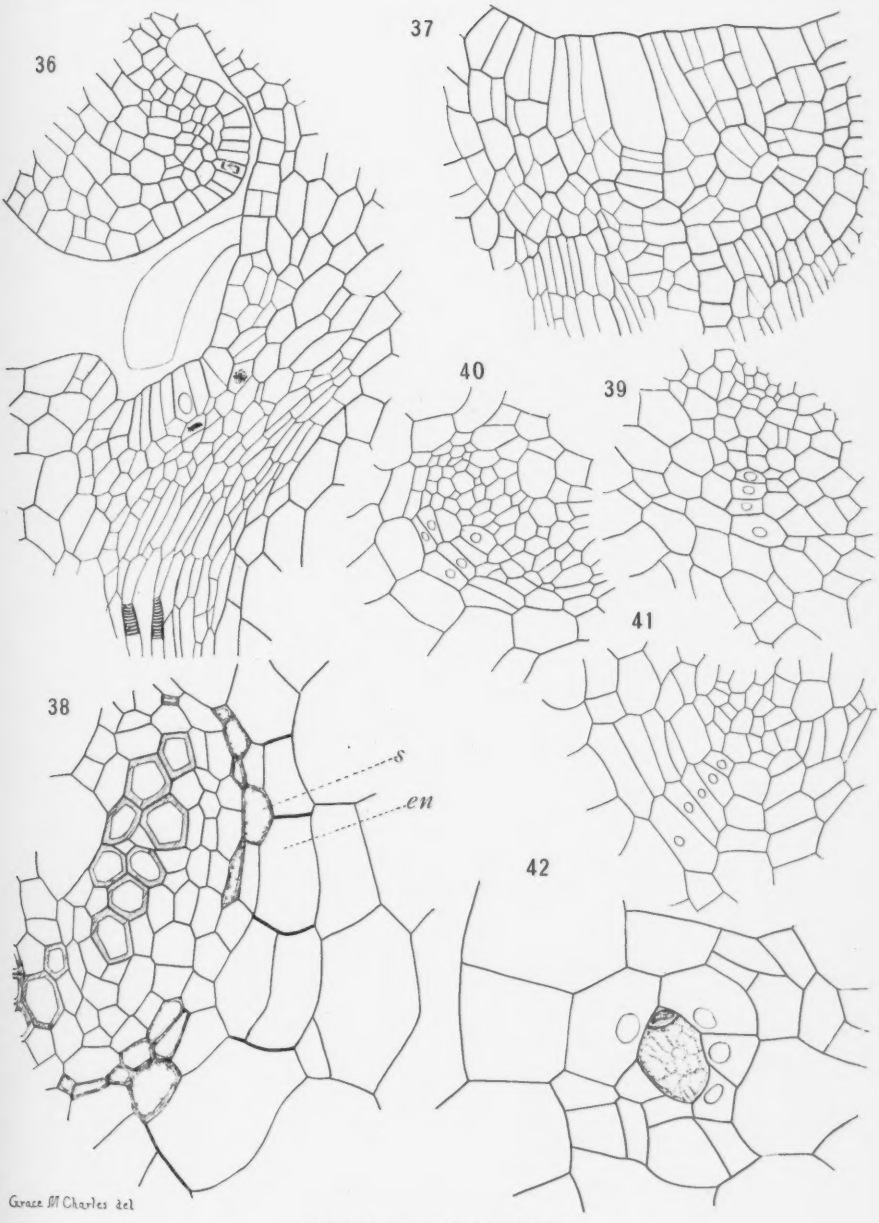


CHARLES on MARATTIA

FIG. 23.—Origin of the medullary strand from the inner surface of a strand of the dictyostele. ×188.

FIG. 24.—Diagram of the strand of the dictyostele at fig. 23, showing the relation of the origins of medullary strand and root trace.

FIG. 25.—Diagram of the vascular cylinder, showing the relation of the medullary strand to leaf gaps and leaf traces.

FIG. 26.—Transverse section of the cotyledonary node, showing the departure of an exarch leaf trace. ×400.

FIGS. 27–30.—Transverse sections of the cotyledonary trace, showing the transition from exarch to mesarch protoxylem. ×400.

FIG. 31.—Transverse section of the apical region of a sporeling with six leaves, showing the triangular apical cell and large segment; at the left above is the youngest leaf trace. ×188.

FIG. 32.—Transverse section of apical region of a sporeling with 25 leaves, showing an irregular apical cell. ×188.

FIG. 33.—Transverse section of an older stem, showing a four-sided apical cell. ×188.

FIG. 34.—Transverse section of a stem 6 mm. in diameter, showing two meristematic blocks of cells. ×188.

FIG. 35.—Transverse section of the apex of a stem 12 mm. in diameter, showing a meristematic region. ×188.

FIG. 36.—Longitudinal section of the apical region of a very young sporeling. ×400.

FIG. 37.—Longitudinal section of the apical region of a stem with 30 leaves; the tissue below the apical cell is pith; at the sides is vascular meristem. ×188.

FIG. 38.—Transverse section of a young stele, showing a frequent relation of sieve tubes to endodermis. ×400.

FIG. 39.—Transverse section near the apex, showing early origin of root from vascular meristem. ×130.

FIGS. 40, 41.—Transverse sections of later stages in the development of roots than fig. 39. ×130.

FIG. 42.—Transverse section of a mucilage duct, showing a cell disintegrating in the mucilage. ×400.

STUDIES ON THE RELATION OF THE LIVING CELLS TO THE TRANSPIRATION AND SAP-FLOW IN CYPERUS. II

JAMES BERTRAM OVERTON

(WITH TWO FIGURES)

Experiments with poisons

In order to kill certain portions of the stems of *Cyperus*, I have used chloroform and ether in the manner described by ROSHARDT, and have always found that the leaves soon droop, behaving exactly like those placed in an atmosphere of these substances. When the fluid is poured into a tube incasing the stem or placed on cotton in the tube, the leaves soon droop. This indicates in my opinion that these substances are soon absorbed and carried to the leaves. The leaves soon fade and wither after treatment with ether or chloroform. I have also made several experiments with xylol in the same way, and found that the results are similar to those obtained by using steam. In one experiment xylol containing eosin was poured into an incasing tube inclosing 15 cm. of a stem 43 cm. high. That the xylol was absorbed by the stem was indicated by the color; at the end of 30 min. the xylol was drawn off and the joints were secured. A plant had been chosen which had a well-developed branch from the base of one of the crown leaves. The involucre remained fresh and turgid for 10 days and then dried, while the branch lived 5 days longer; the part treated with xylol collapsed and the leaves became yellow and dried in about 15 days. The whole behavior of the plant was like that of one which had had a portion of its stem steamed, except that leaves on such steamed plants do not always turn yellow. Other experiments with xylol gave similar results.

I have tried several other poisons in solution, killing 5–10 cm. of the stems by pouring the liquid into incasing tubes. In many cases I have chosen plants with branches developing from the crown. I have used 95 per cent alcohol, 1 per cent chromic acid, saturated

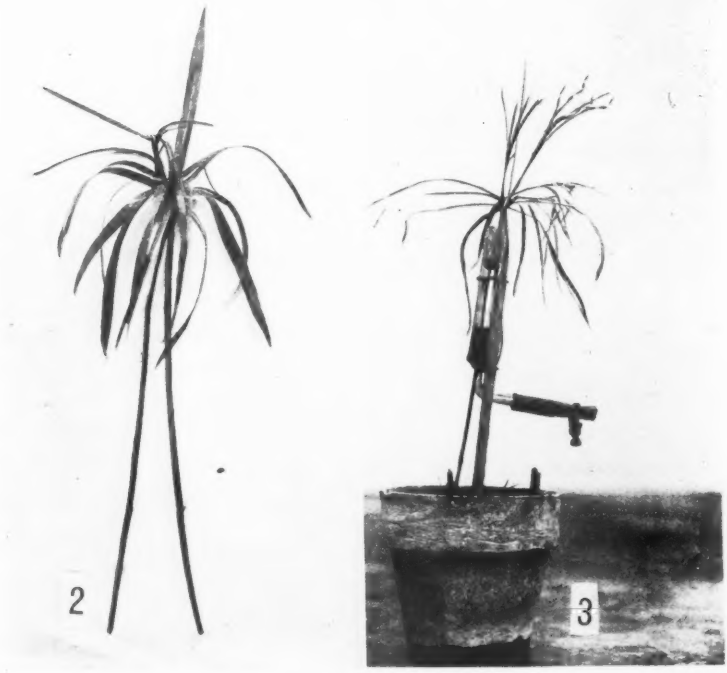
aqueous solutions of $HgCl_2$, $CuSO_4$, and picric acid, Zenker's fixing fluid, KOH, and 40 per cent formalin for 0.5–72 hours.

In one case 10 cm. of a 40 cm. stem were surrounded for 48 hours with picric solution; the involucral leaves drooped in 3 days, but were perfectly turgid and did not become discolored and dry for 26 days, and the branches, which were 10 cm., 11 cm., and 12 cm. long, remained fresh for 44 days. The incasing tube was then removed and the plant was apparently in good condition. The stem was obviously dead, the immersed region being discolored, but there was no contraction of the protoplasts observable. Other experiments with picric acid are described in table X below.

In experiments with chromic acid, $HgCl_2$, Zenker's fluid, formalin, and KOH, the plants very soon faded, although not always losing the turgidity of their leaves immediately after treatment.

By using 95 per cent alcohol and $CuSO_4$ I have obtained some striking results. On April 12 a plant 35 cm. high, with four branches on the crown, was chosen and the stem incased in a glass tube; 95 per cent alcohol was poured into the tube so as to immerse the stem for 9 cm. The lower portion of the treated region was slightly mechanically injured, so that the alcohol could be readily absorbed; that it was absorbed was shown by a lowering of the fluid in the tube. At the end of 48 hours the leaves of the crown had shown signs of drooping and the liquid was removed; after 7 days the crown leaves and two branches were partially withered. Six of the crown leaves faded and yellowed in 10 days, one branch showed one leaf, and one branch showed 2 leaves alive for 6 weeks. The remaining crown leaves continued green, with but portions yellow, and the remaining 2 branches kept on growing, and at this writing (July 18), after 76 days, were 6 and 8 cm. long respectively, having grown about 5 cm. each. Furthermore, 10 days after treatment, 7 new branches started, all of which were growing (July 18). The incasing tube was removed from the stem, and it was examined to be sure a section was dead. As to this there can be no question, as is shown by the photograph (fig. 2). As a result of this examination, it was found that 4 cm. of the stem where injured were entirely brown and the parenchyma disorganized, which appears black in the figure, but apparently no substance had been carried into the

lumina of the vessels. No streaks could be observed above the dead part, as is the case in stems on which steam is used. Apparently



FIGS. 2, 3.—Fig. 2, photograph of a plant which has had a portion of the stem killed with 95 per cent alcohol; stem split lengthwise in order to show the appearance of the dead portion; dead cells appear black in photograph; parenchyma cells almost entirely disintegrated; this figure also shows the healthy crown of leaves and several new branches which have developed since the treatment and which were still growing at the time when the stem was cut; fig. 3, photograph of a plant 63 days after 10 cm. were killed with $CuSO_4$; incasing tube into which the poison was poured still in place; darkened, shriveled stem seen through glass tube surrounded with a plug of cotton; crown shows several leaves still in good condition and the growing branch in center still turgid.

the plant would have remained alive and the stem have continued to conduct sap as long as the injured portion was protected. The dead portion fell to pieces when exposed and touched. From this

experiment, therefore, it seems possible to kill a certain region of the stem without injuring the leaves, and to show that the dead portion is capable of water conduction so long as actual breaking up can be prevented.

The objection may be raised that the killed region in the above experiment was too short to show conclusively that living cells are not necessary for sap-flow. I have succeeded in killing 10 cm. of the stem by another poison without injury to all of the parts above, and thus obtaining results quite as striking. A stem 23 cm. long, with a healthy crown of 11 involucral rays with 2 branches each 8 cm. long and 2 others each 10 cm. long, was surrounded for 4 cm. with a saturated aqueous solution of $CuSO_4$ for 36 hours on May 7. The $CuSO_4$ was absorbed and the stem discolored for 20 cm., or up to the base of the crown. The liquid was removed and a plug of cotton put loosely about the stem in the tube inclosing the upper portion of the 10 cm. which was discolored. On May 20, or after 13 days, the plant was in perfect condition except one branch, some of whose leaves were drying, and the leaf tips of the crown, which showed signs of yellowing. This branch and one of the others finally dried and died, and 3 leaves of the crown died, but the remaining 8 leaves of the crown and the branch have remained perfectly fresh, green, and turgid up to the present writing (July 18); the other branch has grown several centimeters. The stem is partially collapsed, as indicated by its smaller size, and has colonies of mold (*Penicillium*) on it, owing to the fact that the incasing tube was not closely sealed. The stem is dark brown, almost black, and is certainly dead. This experiment shows, therefore, that it is possible for 10 cm. of a dead stem to conduct water for 8 leaves and 2 branches for an indefinite period of time. A photograph of this plant is shown in fig. 3. The results of the above-described experiments appear below in tabular form.

From these experiments with picric acid, alcohol, and $CuSO_4$, we see that it is possible to kill a portion of the stem without completely disorganizing the killed stretch and without interfering with its conducting capacity.

I have further attempted to determine quantitatively the amounts of water that may be evaporated from perfectly dead

TABLE X

SHOWING THE EFFECT OF POISONING 4 TO 15 CM. OF THE STEM WITH XYLOL, PICRIC ACID, ALCOHOL, OR $CuSO_4$

No. of exp.	Height of stem	Distance treated	Time of treatment	Method of treatment	Date	Results and remarks
1—P (1910)...	43 cm.	15 cm.	30 min.	Xylol (and eosin)	April 14	Plant and well-developed branch; involucre remained fresh and turgid for 10 days and branch for 5 days longer; whole plant behaved as though it had had a portion of stem killed by steam; part in tube collapsed and portion killed; leaves yellowed and dried in 15 days.
4—P (1910)...	40 cm.	14 cm.	72 hrs.	Picric acid	April 17	Leaves remained fresh for 7 days; on 8th day leaf tips began to droop, but no signs of withering or fading; plant cut off for examination, acid apparently penetrated stem and carried short distance above place of treatment, but not in leaves, as was shown by color.
5—P (1910)...	35 cm.	4 cm.	48 hrs.	Picric acid	May 3	Plant had healthy crown and one large branch from the crown, 10 cm. long and 2 cm. high; crown leaves drooping in 3 days but turgid and green, showing no fading; May 27, no visible withering or fading; plant cut off and examined; no plugging of the vessels or collapse of parenchyma cells.
6—P (1910)...	40 cm.	10 cm.	48 hrs.	Picric acid	May 3	Plant had good involucre and 3 branches, one 10 cm., one 11 cm., and one 12 cm. long; in 3 days crown leaves slightly drooping, but perfectly turgid; plant still in good condition June 16; removed for examination (see text description).
2—P (1910)...	35 cm.	9 cm.	48 hrs.	95 per cent alcohol	April 12	Plant had 4 branches on crown; crown leaves and 2 branches partially withered in 7 days; in 10 days 6 of crown leaves entirely faded; one branch dry in 10 days; one branch kept one leaf, and one branch kept 2 leaves turgid for 6 weeks; in 10 days after treatment 7 new branches started and were still growing June 18, or 76 days after treatment; stem in tube brown and apparently dead, but not collapsed; cut off for examination; stem fell to pieces where killed.
11—P (1910)...	23 cm.	10 cm.	36 hrs.	Saturated aqueous solution of $CuSO_4$	May 7	Plant had good crown with 2 branches, each 10 cm. long, and 2 others each 8 cm. long; May 15, plant in perfect condition except leaf tips very slightly yellowing; all branches normal; May 20, plant in good condition except one branch; July 9, remaining branches in good condition and growing; July 12, one of remaining branches withered.

plants. It was at once found that the kind of poison used to kill the plant very greatly influences the amount of water evaporated, and that in many cases the amount of water evaporated greatly exceeds the amount transpired by a living plant of the same size and under the same conditions. Cut stems were placed in chromic acid, picric acid, and $HgCl_2$ for 24 hours, until it was certain from their appearance that the poison had been carried to the leaves and that the whole plant was killed; they were then transferred to distilled water. All of the plants in table XI had 17 leaves, each of the same size, age, and area. The area of each plant in table XII was about three times that of each of the plants in table XI, 21 large leaves being on each. Plants of approximately the same leaf areas and of the same stage of development were chosen for controls. The amount of water evaporated from each plant was determined by weighing. Tables XI and XII give the results of my experiments on this point.

TABLES XI AND XII

SHOWING VARIATIONS IN THE DAILY AMOUNTS OF EVAPORATION FROM PLANTS COMPLETELY KILLED BY CHROMIC ACID, PICRIC ACID, OR $HgCl_2$, AS COMPARED WITH A CONTROL PLANT IN WATER

TABLE XI

No. of plant	Fluid	Loss per day in grams										Average loss per day	Percentage of water in plant on 10th day
		1	2	3	4	5	6	7	8	9	10		
I ..	H_2O	0.1	0.9	0.6	0.5	0.5	0.5	0.1	0.4	0.3	0.5	0.44	81
II ..	Chromic	0.1	0.9	0.8	0.8	0.9	0.6	0.5	0.7	0.9	0.5	0.67	36
III ..	$HgCl_2$	1.2	1.1	1.7	1.6	1.5	1.1	0.8	0.9	1.1	1.3	1.23	28
VI ..	Picric	0.7	0.5	0.4	0.4	0.5	0.6	0.4	0.4	0.2	0.4	0.45	11

TABLE XII

No. of plant	Fluid	Loss per day in grams										Average loss per day
		1	2	3	4	5	6	7	8	9	10	
I.....	H_2O	7.4	5.1	3.0	0.9	0.6	0.6	*	*	*	0.5	1.8
II.....	Chromic	2.6	2.9	2.7	2.4	2.5	2.5	*	*	*	3.4	1.9
III.....	$HgCl_2$	7.0	7.6	7.0	6.6	6.5	6.5	*	*	*	10.4	5.2
IV.....	Picric	2.5	1.1	2.7	0.9	2.6	1.8	*	*	*	4.4	1.6

*Impossible to take readings on these days, but does not affect average.

The stems were cut off under water and allowed to remain there for 6 hours, after which they were quickly transferred to the poisons; in each case the base of the stem was immersed for a distance of 5 cm. They were then transferred to bottles containing distilled water, which was covered with a layer of olive oil to prevent surface evaporation. Weighings were made daily at noon for 10 days.

It will be seen from these tables that more water is evaporated from a perfectly dead stem of *Cyperus*, killed with chromic acid, picric acid, or $HgCl_2$, than from a cut plant set in water and kept under the same conditions. These substances in some way apparently alter the constitution of the plant so as to allow it to give off more water. As shown by these tables, a plant cut under water and kept standing in water continually falls off in the amount of water transpired from day to day, and very seldom increases the quantity given off on a certain day over that transpired the previous day. In the case of poisoned plants the reverse is true. Noting the plants numbered II in each table, an increase over the first day is shown on each of the two succeeding days. The amount of water evaporated on the 8th and 9th days exceeds that of the 7th. Certain other days show increases over the preceding days. The plant killed with $HgCl_2$ gives off a quantity of water far in excess of that given off by plants killed by the other two poisons. In table XI plant no. III gives off nearly three times as much water on the average per day as does no. I. Another noticeable fact is that although these poisoned plants evaporate comparatively large quantities of water, the percentage of water contained in the plant is very much below that in plants which have not been killed. This is shown in the last column of table XI; the plant in water contains 81 per cent of water, while the one killed with $HgCl_2$, which gave off the largest quantities of water, contained only 28 per cent of its dry weight of water.

General discussion

As shown by BOEHM (**3**), STRASBURGER (**30**), URSPRUNG (**32–37**), DIXON (**9–12**), ROSHARDT (**24**), and my own experiments, the leaves above a steamed or otherwise heated portion of the stem

being kept in connection with the roots remain for a considerable period turgescent, but sooner or later wither and die. This is very distinctly shown in table IV, from which data it was concluded that the leaves above a steamed portion never remained longer than 18 days without withering. This was shown to be true when only 5 cm. of the stem were steamed, while the leaves remain turgid for 3 days only when 30 cm. were killed. It has been shown that in *Cyperus* sufficient water to maintain the turgidity of the leaves for 3–18 days will rise through a stem 15–60 cm. high with a section 5–30 cm. long, which has been killed by steam. It has also been shown that sufficient water to keep the leaves turgescent for 3 months can ascend through a stem 23 cm. high when 10 cm. are killed with $CuSO_4$. It follows from my observations that the leaves wither above a longer heated stretch faster than above a shorter one, as has been observed by JANSE, URSPRUNG, DIXON, and ROSHARDT. It is further evident that when short portions of the stems are steamed (5–10 cm.), the leaves above do not wither quite as quickly as those on stems cut from the same plant and placed in water under the same conditions of light, temperature, and air moisture. Leaves cut and not placed in water always lose their turgidity and dry long before those on steamed stems, regardless of the length of the killed portion. Such cut branches lose their turgidity in 1–2 hours, and become completely dry in 24–48 hours. The fact that the leaves on heated stems remain longer turgid than those cut and left in air shows that a certain amount of water passes through the killed portion, as is also admitted by URSPRUNG. This is also clearly shown in a quantitative way, by comparing the transpiration after killing a certain portion of the stem with steam with that before the steam was applied. Such a comparison is brought out in tables V and VI. The amount of water passing through such a steamed stem rapidly diminishes, falling off almost immediately from 80 per cent to 50 per cent of the dry weight of the leaves, until the leaves become air dry, when they still contain about 11 per cent of the dry weight of water.

URSPRUNG'S conclusion from such experiments, that living cells are necessary for sap-flow, is certainly not obviously necessary. The long period during which the leaves remain turgid in his own

experiments certainly suggests that the death of the stem cells does not operate in any direct fashion to cut off the water supply. Such a period as 18 days gives opportunity for the development of all sorts of secondary causes, to which the final death of the leaves may well be due. That the amount of water carried is at once reduced may just as well be due to gross mechanical changes secondarily produced in the tissues as to the death of the cells.

DIXON calls attention to the fact that the investigators who first observed the withering of the leaves above a heated portion of the stem, such as WEBER (**40**) and JANSE (**16**), did not attribute the phenomenon simply to the lack of activity of the dead cells of the stem, but to a possible blocking of the vessels, which thus diminishes the water supply. It is certain from the methods which I have used to protect the steamed portions of the stems, that the diminished water supply which reaches the leaves after treatment cannot be due to a lateral evaporation from the heated stretch. The carefully sealed incasing glass tubes preclude such a possibility. URSPRUNG has also concluded from his experiments that the wilting of the leaves above a killed portion of the stem is not due to a lateral evaporation from the heated portion.

In the experiments whose results are shown in tables VIII and IX, there was an increased amount of water transpired on certain days after a section of the stem was killed with heat. It appears, therefore, that URSPRUNG'S statement that the fading of the leaves above a killed portion is a sure index that insufficient water supply reaches them is not proven, and that the wilting may well be due to deleterious substances being introduced into them from the dead cells. Although the plant described in table IX had an increased amount of water ascending to the leaves, they finally withered while still giving off large quantities of water. I am forced to agree with DIXON (**10–12**) that URSPRUNG'S interpretation of these phenomena is an arbitrary one. As noted above, DIXON ascribes the earlier wilting of the leaves on stems, a section of which has been killed with heat, to a possible clogging of the vessels, which hinders water passage, or to a breaking of the water columns due to the heat used, which may thus interrupt the continuity of the flow. He holds, however, that the withering of the leaves is due chiefly

to the action of poisonous or plasmolyzing substances in them, which interferes with the osmotic action of the cells and thus inhibits their lifting power. URSPRUNG regards this suggestion as an empty conjecture.

My results agree well with those of ROSHARDT, except that in the plants treated with steam I have never observed an increase in the amount of water given off during any one period over that in the preceding, such as is shown by ROSHARDT's table. It appears to me that if the living cells of the stem are necessary to the ascent of water, as ROSHARDT contends, there could not possibly be an increased amount of water transpired during any one interval over that of the preceding. The general gradual falling off in the amount of water transpired after killing a portion of the stem, which ROSHARDT records, agrees with my observations on *Cyperus* under similar circumstances, except that the diminution in the amount of water lost, after steaming a section of the stem, is continuous. I feel that the cause is the same in both cases, namely, a stoppage of the vessels, which I have actually shown to occur in *Cyperus*, and a probable injury to the leaves due to deleterious substances being introduced into them. It seems to me that ROSHARDT has placed exactly the opposite interpretation on the results of his quantitative experiments to that which they really show.

Microscopical examinations of the stems of *Cyperus* above a steamed stretch show that some of the vessels are plugged for a considerable distance with a brown, gumlike gelatinous mass, which reacts to alkanin like resin. This substance is insoluble in water and often stops the vessels throughout the length of the stem above the killed portion, even plugging some of the tracheae of the leaves. There can be no doubt that this stoppage of the vessels in *Cyperus* accounts in a large measure for the immediate and constantly diminished water supply which reaches the leaves above a steamed portion of the stem. The discoloration of the contents of the sieve tubes is conspicuous, and suggests that the steaming causes considerable disorganization, which may be the source of the resinous substances in the vessels. Although URSPRUNG observed stoppage in several plants, he thinks that the

diminished water supply cannot be due to this, since the leaves do not wither at once, but remain for some time turgid. I have described the progressive effect which steaming the stems of *Cyperus* has on the withering of the leaves, but I attribute this progressive injury, which finally results in the death of the leaves, to the introduction of injurious substances from the dead cells. The presence of these poisonous or plasmolyzing substances seems to account for the final withering or drying of the leaves. The leaves first die and then dry, as DIXON puts it. The leaves do not die from lack of water supply, as URSPRUNG would have it, but because they are killed.

Not only are the cavities of the vessels plugged with a brownish mass, but the walls of the conducting tubes are tinged with yellow. It seems quite probable that the presence of some substance in the walls of the tubes may lessen their power of conduction also. DIXON (**10–12**), as noted, has observed the presence of a substance which stains the walls of the vessels and thinks that "it would be hard to believe that the deposit of this colored substance in the walls and lumina of the tubes could be without effect on their efficiency in transmitting water." I have already described a similar brownish appearance of the walls of the vessels as well as the plugging of the lumina for some distance above the cut end of a stem of *Cyperus* standing in a sterilized decoction of the same plant. SCHWENDENER'S (**28**) researches, tending to show that heating the stem does not change the physical character of the cell walls of the tubes, and that the micellar structure and imbibitional power is not affected by such treatment, probably do not take sufficient account of the action of poisonous substances caused by heating the stem on the structure of the walls of the vessels and the efficiency of their conductivity. From my experiments it is clear that changes in conductivity and in the amount of evaporation are brought about by killing the plant with such substances as chromic acid, picric acid, and $HgCl_2$, often accelerating evaporation to a very marked degree.

I have repeatedly shown that when stems are set in a decoction of the same plant, the leaves wither much earlier than those set in water. Additional evidence that injurious substances are engendered by heating the plant was obtained by growing *Cyperus*

plants in nutrient solutions containing a decoction. As noted above, the plants grown in such solutions began to droop in 3–5 days, showing discoloration and fading along the veins in 7–8 days, while control plants grown in nutrient solutions without the decoction remain perfectly normal. DIXON'S experiment, in which leaves normally supplied with water together with water from a heated side branch were shown to soon wither, seems to me quite decisive proof that deleterious substances enter the leaves from the killed portion. URSPRUNG (**35–37**), however, was unable to produce the same effect on the leaves of *Impatiens* by using DIXON'S method.

Microscopical examination of the leaves from a stem killed by heat show in certain regions a discoloration of the mesophyll cells, the protoplasts being contracted and the chloroplasts being discolored. The leaves of plants grown in decoctions also show similar conditions. DIXON (**10–12**) also found disorganization and discoloration of the mesophyll cells of the leaves above a killed portion, and, as noted, even on a separate branch if some of its water supply passes through a heated region. In these cases it certainly appears that the leaves are drying not so much for lack of water as from injury and death of the cells. The observation of SCHROEDER (**27**) that most leaves can lose 50 per cent of their fresh weight without injury is further proof that leaves above a heated portion of a stem do not wither on account of the diminished water supply. In the microscopical examinations which I have made of leaves from steamed stems, I have found many of the conditions described by SCHROEDER in his studies on the symptoms of death as a result of wilting, namely, the contraction of the protoplasts of the mesophyll, and the change in color and rounding up of the chloroplasts. The fact that the plant killed with steam constantly decreases in the amount of water given off is also in harmony with SCHROEDER'S observations. The first 50 per cent of the leaf's fresh weight is very rapidly lost when dying, as he shows, after which the amount lost decreases uniformly. My experiments, in which the amount of transpiration was determined after killing a portion of the stem with steam, show that there is in the first 2 or 3 days a very rapid and immediate decrease in the water loss, and that then the rate of transpiration

decreases more uniformly. These facts, taken together with the appearance of the mesophyll, seem to show beyond question that the leaves on a steamed stem are dying, and that death is not entirely due to a lack of water.

Applying heat by means of wax heated to 110° C. does not cause so much discoloration of the contents of the sieve tubes, or so much stoppage of the lumina of the vessels, and the mesophyll of the leaves does not show so much immediate plasmolysis. The leaves above stems so treated remain turgid three times as long as those on steamed stems. Plants do not show such an immediate decrease in the transpiration as is the case when the stems are killed with steam. The effect upon the transpiration rate and upon the injury to the leaves in using hot wax is not a progressive one, as it is when steam is used. Altogether the method of using hot wax to kill a section of the stem seems more satisfactory than steaming, with reference to the question of the relation of the living cells to sap-flow. And it is still plainer in stems killed in this way that the death of the stem cells does not *per se* directly affect the sap-flow.

My experiments with poisons, in which 5–10 cm. of the stem were treated for 36–72 hours, show that it is possible to kill a portion of the stem without completely disorganizing the killed stretch and without reducing its conducting capacity. Not only does a sufficient quantity of water pass through the poisoned portions to supply the transpiration needs for a comparatively long period of time (3 months in the case of $CuSO_4$), but also to allow the development and growth of new parts. As has been shown, the mesophyll cells remain perfectly normal; no discoloration of the chloroplasts and no contraction of the protoplasts follow this method of treatment, if care is taken that the poison does not reach the leaves. In the poisoned portion of the stem the cells are apparently "fixed" when alcohol or picric acid is used, there being no plasmolysis. When $CuSO_4$ is used, the parenchyma of this region has its protoplasts contracted, but the vessels remain normally open and apparently unaltered.

From my experiments, in which poisons were used to kill the whole plant, it was at once evident that the kind of poison greatly influenced the subsequent rate of evaporation of water from the

whole plant, and that in many cases the new rate far exceeds the normal transpiration of a plant of the same age and superficial area under the same conditions. In these cases it is plain that the tissues are ruptured so as to expose additional cell surfaces to the atmosphere.

DIXON and JOLY (**13**) consider that capillarity or imbibition of the mesophyll cell walls sets up a suction, aiding the osmotic suction in extracting water from the adjacent vessels. In the case of the poisoned leaves of *Cyperus* there can be no osmotic action of the cells. The imbibitional action of the cell walls, as conceived by DIXON, may however still keep the walls wetted, and the suction from the evaporation may be transmitted to the cohering water columns of the vessels. DIXON (**11**) points out that the point of support for the tensile strength in the case of transpiring dead organs is always the walls. He thinks that the presence of soluble substances on the outer surface of the walls would function also in maintaining the suction. Perhaps the condensation of the metallic salts of these poisons on the outer surfaces of the cell walls act in this manner.

BOEHM (**4**) formulated a theory of sap-flow based entirely upon capillarity, maintaining that the capillary attraction between the walls of the conducting tracts and the water is greater than obtains in a glass tube of the same diameter. The experiments of STRASBURGER (**30**), however, show that in the vessels of *Aristolochia* the capillary ascent of water is much slower than in glass tubes of the same diameter. It seems quite possible that $HgCl_2$, and some of the other poisons used by me, which cause an increased amount of evaporation, as is shown in tables X and XI, may in some way alter this capillary relation so that the water may flow faster in such poisoned tubes. Cells without turgor, that is perfectly dead cells of the leaves, are able to raise water to a considerable height. STRASBURGER showed that rather tall trees with poisoned leaves are able to raise water 22 m. ASKENASY (**1**) found that cut branches of *Taxus* and *Viburnum*, whose lengths he does not mention, which had lain for a long time in boiling water or in alcohol and were completely dead, could suck up water and eosin. BOEHM (**4, 5**) also showed that water could rise in a dead

branch when the leaves were dead. A cooked and dried oak twig about 25 cm. long was then set in a tube with a manometer, with water above and mercury below. The twig was able to raise mercury 70.3 cm. high. In another somewhat modified experiment with a *Thuja* twig the mercury rose to 86.4 cm.

ASKENASY believes that the suction power exhibited by dead leaves is explainable by the fact that the water evaporates from the outer surface of the cell walls of the mesophyll into the intercellular spaces, and is supplied from within through the protoplasmic lining. He thinks that the imbibitional force of the wall is greater than the osmotic power of the cell sap. He further adds:

> Da diese Imbibitionskraft durch den Tod der Zelle im Allgemeinen nicht beeinträchtigt wird, so ist es kein Wunder, dass auch tote Zellen, wenn sonst die Verhältnisse günstig liegen, im Stande sind, das an ihnen verdunstende Wasser ebenso hoch zu heben wie lebendige.

There can be no doubt that cell walls possess a great attraction for water. As DIXON (**10–12**) points out, the submicroscopical spaces occupied by the imbibed water in the cell walls of the mesophyll are intensely minute capillaries. It seems quite possible that these poisons may in some way alter the character of these passages, and so affect the amount of water imbibed by the walls and also the amount of water evaporated by the surfaces of these cells. It is certain that in the case of plants poisoned throughout, the elevation of the water in the stems, and its evaporation from the leaves in larger quantities than normally occurs in living plants, depend purely upon physical processes.

Summary

1. Stems of *Cyperus* cut and placed in water wither sooner than when a certain portion, not to exceed 20 cm., has been killed by steam.

2. When 20 cm. of the stem are killed by steam, the leaves wither in about 8 days, that is, in about the same time as the control plants.

3. The longer the portion of the stem killed with steam, the sooner the leaves above wither and dry. When 25 to 30 cm. of the stem are killed with steam, the leaves wither in 3–5 days.

4. No matter how long the section killed may be, the leaves on steamed stems never wither quite so quickly as those cut and not placed in water, but under the same conditions of light, temperature, and air moisture.

5. In *Cyperus* sufficient water to maintain the leaves turgid for 3–18 days will rise through a stem 15–60 cm. high, with a section 5–30 cm. long which has been killed with steam.

6. A certain amount of water is raised through the steamed portion, but it gradually diminishes in quantity from day to day, until the leaves become air dry (about 11 per cent of their dry weight of moisture).

7. The diminished water supply is partly due to a partial blocking of the vessels with a gumlike or resinous substance, which probably owes its origin to the disorganization of the contents of the sieve tubes caused by heating the stems.

8. The withering of the leaves above a steamed portion of the stem is probably caused more by the action of deleterious substances introduced into them from the dead cells than from lack of water. These poisonous substances are probably disorganization products caused by heating with steam.

9. The leaves of rooted plants, grown in nutrient solutions containing sterilized decoctions of the same plant, droop in 3–5 days, discolor and dry in 7–8 days.

10. The withering leaves above a portion of the stem killed with steam show all the symptoms of dying, namely, rapid loss of water after treatment, then a more uniform loss, rounding up and discoloration of the chloroplasts, and contraction of the mesophyll protoplasts. The leaves are apparently drying, not so much from lack of water as on account of the death of the cells from other causes.

11. Judging from the behavior and disorganization of the leaves on a stem, a section of which has been killed with steam, it is evident that this method of killing the cells is not a satisfactory one in order to settle the question as to the relation of the living cells to sap-flow.

12. Killing a portion of the stem by applying wax heated to 110° C. causes less apparent disorganization of the cells, less injury

to the leaves above, and does not cause a marked immediate decrease in the transpiration.

13. Experiments in which 5–10 cm. of the stem are killed by treatment with picric acid, 95 per cent alcohol, or $CuSO_4$, for 36–48 hours show that sufficient quantities of water may ascend through the poisoned portions to supply the transpiration need for a comparatively long period (90 days), and to allow the development of new branches.

14. Certain poisons (picric acid, chromic acid, and $HgCl_2$) may greatly accelerate the amount of water evaporated in poisoned plants. Not all poisons act alike in this respect; $HgCl_2$ causes the greatest amount of increase in water loss.

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REDUCTION BY ROOTS[1]

OSWALD SCHREINER AND M. X. SULLIVAN

The roots of many plants, such as wheat, have an oxidizing power (1). This property is readily shown by certain chromogens, alphanaphthylamine, benzidine, phenolphthalin, aloin, guaiac, pyrogallol, etc. When chromogens like alphanaphthylamine and benzidine are used, the colors due to oxidation are shown on the root itself. The most marked oxidation is shown by a narrow but very distinct band of color just back of the root cap. Then comes a practically colorless zone and then a broad colored zone, the color becoming less intense toward the upper part of the root.

In regard to the practically colorless zone or the zone with little color just back of the region of intense coloration, it seemed as if the lack of color might be due to a reducing power, a reductase or possibly an antienzyme.

The possibility of an antienzyme is suggested by the work of BERTEL (2), who showed that with the exclusion of oxygen there accumulated in the cells of the lupine roots larger quantities of tyrosine than are usually found. The tyrosine which arises from the protein degradation in the early stages of the seedling's growth is normally oxidized by the enzyme tyrosinase to homogentisic acid and oxidation products of the latter. With the exclusion of oxygen, this oxidation is retarded and tyrosine accumulates.

Subsequently CZAPEK (3) showed that "a short time after the beginning of geotropic induction there appears a retardation of the normal destruction of tyrosine to be recognized by an accumulation of homogentisic acid." The cause of this retardation he attributed to the development of specific antioxidase which inhibits the normal activity of the oxidase of the root tip.

Reducing properties have been found in animal organs, in microorganisms, and in plant juices. The reducing power of the animal organism was shown first by EHRLICH (4), who used alizarin

[1] Contribution from the Laboratory of Soil Fertility Investigations. Published by permission of the Secretary of Agriculture.

blue and the more easily reduced indophenol blue, both of which on reduction give colorless bodies. On injecting these colored substances he found that organs of the animal could reduce them to the leuco-bases. EHRLICH divided the organs of the body into three main groups: (1) those highly saturated with oxygen in which indophenol blue remains; (2) those in which indophenol blue, but not alizarin blue is reduced; (3) those of highest oxygen avidity, in which alizarin white is formed.

In the first group are the gray matter of the nervous system, heart, part of the muscular system, and kidney capsule; in the second group, most of the muscular system, glands, and connective tissue; in the third group, the lungs, liver, fat, Harder's gland, and mucosa of the stomach.

Since EHRLICH's experiments, the reducing power of animals, plants, and microorganisms has been extensively studied. The reagents used to demonstrate the reducing power are numerous. Among them are various colored substances which form leuco-bodies, such as lacmus, methylene blue, indigo carmine, indigo blue, gentian violet, methyl violet, rosaniline, etc.; nitrates, which are reduced to nitrites; sodium selenite and sodium tellurite, which are reduced to metallic selenium and tellurium. Methylene blue and lacmus are used most. The former is converted to a leuco-base by the addition of hydrogen, the latter apparently by the abstraction of oxygen.

Reduction has been studied more extensively in the case of microorganisms than in animals and plants. Whether the reduction produced by microorganisms is due to enzymes or not has not yet been settled. ROZSAHEGYI (**5**), BAGINSKY (**6**), MÜLLER (**7**), and WOLFF (**8**) believe that the reduction is caused by external metabolic products; while CAHEN (**9**), SPINA (**10**), SMITH (**11**), KLETT (**12**), MAASSEN (**13**), and CATHCART and HAHN (**14**) regard it as an attribute of the bacterial cell. They all agree, however, that the reduction is associated with the development of bacteria.

In regard to reduction in higher plants, it might be mentioned that BINZ and SCHULZ (**15**) found that plant protoplasm had the power of reducing arsenic acid (As_2O_5) to arsenious acid (As_2O_3), while plant protoplasm treated with boiling water lost this power

to a great degree. REY-PAILHADE (**16**) extracted from yeast cells by means of alcohol a substance which would form H_2S from S. To this substance he gave the name philothion. He found it likewise in fresh animal tissues, in the tips of young shoots of asparagus (**17**), and in various grains and young seedlings (**18**). POZZI ESCOT (**19**) verified REY-PAILHADE's work and succeeded in hydrogenating in addition metallic selenium and phosphorus. PALLADIN (**20**) found a reductase in wheat shoots and concluded that it played a part in respiration. DELEANO (**21**) found a reductase or hydrogenase in the albumen of *Ricinus communis*, but not in the roots or the plantules. The albumen triturated with sulphur gave hydrogen sulphide. LAURENT (**22**) showed that young seedlings reduce nitrates and that there can be extracted from plants an unorganized ferment which has the power to convert nitrates to nitrites. ABELOUS and ALOY (**23**) found a nitrate-reducing enzyme in potato tubers. KASTLE and ELVOVE (**24**) confirmed the presence of the nitrate-reducing enzyme in the potato and showed that it was present also in the fruit of the egg plant (*Solanum melongina*). Recently IRVING and HANKINSON (**25**) have found nitrate-reducing enzymes in certain water plants.

Since little has been done upon the reducing power of seedlings growing in soil or solutions, experiments were made to determine the power of the intact and growing roots, especially of wheat, to reduce substances, with the ultimate purpose of seeing if, like the oxidative power, the reducing power would be found to play a significant part in soil fertility.

Various dyes such as methylene blue, indigo carmine, Bismarck brown, gentian violet, etc., were first employed to see if the roots would decolorize the solution in which they were growing. The color of dilute solutions of the dyes was greatly lightened by the growing roots, especially if air was excluded. Since, however, more or less of the dye-stuff was deposited on the outer surface of the root and root hairs, such solutions were not considered satisfactory for showing reduction if this occurs.

STARCH IODIDE SOLUTION.—When wheat seedlings are placed in dilute solution of blue starch iodide with seeds and roots in the solution, the blue color is soon discharged. With the roots only in

the starch iodide solutions, the color is discharged slowly. The addition of hydrochloric acid to the decolorized solution brings back the blue color. Reducing agents such as sodium thiosulphate, formaldehyde, hydrogen sulphide, etc., behave similarly.

Seedlings were kept in water solution of iodine of 0.012 per cent strength of iodine for two hours with: (*a*) seeds and roots in iodine solution; (*b*) roots only in iodine solution; and (*c*) control in which no plants had been. Solution (*a*) gave no color on addition of the starch; (*b*) gave a slight blue color; and (*c*) gave a deep blue.

On addition of a few drops of concentrated hydrochloric acid, all the solutions became deep blue and no difference could be seen in the depth of color. It would seem then that the plants hydrogenate the iodine, forming an iodide from which the acid liberates the iodine, or that the plants in some way render the iodide inactive toward the starch.

Since the chemistry of the starch iodine combination is not sufficiently known, and since the intensity of color produced by the reaction between starch paste and iodine is by no means quantitative, the effect the seedlings had on this reaction was taken merely as a sign of the possibility of a hydrogenase or a reductase in the seedlings, seed, or root.

SULPHUR.—The roots and the seed and roots of the intact seedling were put in contact with well washed, precipitated sulphur, neutral, made slightly acid with hydrochloric acid, or slightly alkaline with sodium hydroxide. In no case was hydrogen sulphide detected by means of lead acetate paper. Alcoholic extracts of the crushed seedlings after the method of REY-PAILHADE (**16**), and POZZI-ESCOT (**19**) were likewise found to have no hydrogenating action on precipitated sulphur.

HEFFTER (**26**) found that compounds containing the sulphydryl or SH group such as thiophenol, benzylmercaptan, ethylmercaptan, thioglycolic acid, and cystein reduce sulphur, and came to the conclusion that the reducing power of cells is due to the labile hydrogen of sulphydryl compounds which give up their hydrogen and become disulphides. This sulphydryl group is present in certain albumins, and is shown by a purple-red coloration with

sodium nitroprusside and sodium or ammonium hydroxide. The crushed wheat roots or seedlings do not give this reaction. According to HEFFTER, non-reducing albumins can be changed to reducing albumins by treatment with a 10 per cent sodium sulphite solution for 12–24 hours and will then give the nitroprusside reaction.

Wheat seedlings of different stages of development from three to ten days old were rapidly crushed, covered with a 10 per cent solution of sodium sulphite, and kept at 40° C., with repeated shaking. The solutions with suspended matter were tested after 2, 6, and 24 hours, and at no time gave the nitroprusside reaction for the sulphydryl group nor did they reduce sulphur. In 24 hours the seedling pulp was tested for the sulphydryl group with negative results, and the pulp formed no hydrogen sulphide from freshly precipitated sulphur.

NITRATES.—To test the power of wheat seedlings to reduce nitrates to nitrites, the wheat grains were treated with a 0.1 per cent solution of mercuric chloride for 30 minutes, and the seeds, well washed with sterile water, were placed in sterile tubes containing a little water. In the tubes tightly closed with cotton the wheat germinated and grew well. There were added to each tube 10 cc. of a 1 per cent solution of potassium nitrate, and after 24 hours the solution was tested for nitrites by means of Griess reagents (**27**), sulphanilic acid and naphthylamine acetate. The ungerminated seeds, whether sterilized or not, did not give the nitrite test under these conditions. The solutions containing the seedlings, on the other hand, gave good tests for nitrites. The ability of sterile seeds germinated in tubes to form nitrites from nitrates was tested several times, both in air and in vacuum. Sometimes a fair amount of nitrite was formed, in one case as high as 6 parts per million, sometimes the amount was very little. It should be borne in mind, however, that nitrites are absorbed by plants. The formation of nitrites was greater in vacuum. It would seem that a nitrate-reducing power appears in the early stages of the wheat seedling, but is not in the seed at rest. The formation of nitrites is small, and no culture tests were made to show that microorganisms were entirely excluded in the experiment. It may be said, however, that enzymes capable of reducing nitrates have been reported in

plant tissue by LAURENT (**22**), ABELOUS and ALOY (**23**), KASTLE and ELVOVE (**24**), and IRVING and HANKINSON (**25**). LAURENT claims that young seedlings of maize, white lupine, and peas have a reducing action on nitrates, while IRVING and HANKINSON have found that a number of plants reduce nitrates more or less.

SODIUM SELENITE.—Sodium selenite was next employed as a test solution. Solutions of sodium selenite of 0.25 per cent were first used. The solutions reacted alkaline to litmus and phenolphthalein, and were toxic to the young seedling. When neutralized by hydrochloric acid, however, the toxicity of the selenite was greatly lessened. When seedlings were grown in the sodium selenite solution made neutral or slightly acid to phenolphthalein and of a strength of 0.125 to 0.25 per cent, the parenchyma cells of the end of the root cap were colored an intense pink in a few hours, varying with the seedlings, by the deposit of selenium. This deposit was more marked in slightly acid solutions. The points of emergence of the secondary roots were likewise colored. Later the whole root became colored.

SODIUM TELLURITE.—When sodium tellurite is used as a test for reduction, the roots are colored a blue-black by the deposit of metallic tellurium, otherwise its behavior is like that of sodium selenite.

These experiments show conclusively that the intact roots possess a reducing power. This reducing power is stronger in the young seedling, being much stronger in the seedling 4 days old than in the seedling 12 days old. As judged by the quickness with which the deposit of selenium is made on the roots and the extent and intensity of the deposit, the reducing power increases from time of germination to the sixth or eighth day and then decreases. It is still present in seedlings 13 days old, the oldest seedlings examined. The oxidizing power of the wheat seedlings, on the other hand, as judged by the oxidation of aloin, is less in the young seedling and increases with age, being considerably greater in the twelve-day seedling than in the six-day seedling, and still greater than in the case of the four-day seedling.

Dying tissue tends to have a reducing action. The reducing action of the wheat roots on sodium selenite, however, is not a

death phenomenon, since (1) roots killed by being dipped in boiling water have no reducing action on the selenite; (2) the roots in toxic non-neutralized sodium selenite do not reduce; (3) intact roots boiled in solution of sodium selenite have no deposit of selenium upon them; (4) the root ends being cut off and the injured root placed in the selenite solution, the deposit of selenium is not on the cut end but at the point of emergence of the secondary roots.

The reducing power of the wheat roots on sodium selenite is checked by acids and alkalies and by toxic organic matter. It is stimulated by faintly acid reaction and by light. The observable action of salts on the reducing action is variable on account of lack of precision of method, though as a rule sodium nitrate solution equivalent to 50 p.p.m. NH_3 gives the quickest and heaviest deposit at the root tip, while potassium salts give the heaviest deposit on the rest of the root. Potassium salts containing 50 p.p.m. K_2O appeared to retard reduction slightly at the root tip. Potassium iodide containing 14.5 p.p.m. K_2O, however, stimulated reduction.

Incidentally it is of interest here to state that potassium retards greatly the oxidation power as indicated by aloin, and that a slight acid reaction stimulates reduction while inhibiting oxidation, thus seeming to show that the reducing and oxidizing powers are not necessarily concomitant.

Whether or not the reducing power of the wheat roots on sodium selenite is due to enzyme activity, it is hard to say positively. In regard to the enzyme nature of the reducing agent in animal cells, HEFFTER (**26**) concluded that there were two groups of reduction processes. One group was hardly influenced by hydrochloric acid or by heating. This group embraced the formation of hydrogen sulphide from sulphur, the reduction of arsenic, tellurium, and selenium compounds, the reduction of cacodylic acid and of different dye-stuffs. These reductions he believes are caused by the labile hydrogen of the sulphydryl group of certain albuminous bodies. The other group of reduction processes, such as the change of nitrates to nitrites and of nitrobenzol to amino combinations, were restrained by heat. This group of reactions he thought at first might be enzymotic, but later he came to the conclusion (**26**) that they likewise were non-enzymotic.

Whether enzymotic or not, the reducing action on sodium selenite is most marked intracellularly in the parenchyma cells of the root tip. The primary localization of the deposited selenium in the root tip speaks neither for nor against the enzyme nature of the reducing power.

Reduction of sodium selenite may be brought about by purely chemical means. Thus GRÜSS (**28**) found that lactic acid could precipitate selenium from sodium selenite. Lactic acid we have found to have no reducing action on sodium selenite of a strength of 0.25 per cent, but has some reducing action on a 4 per cent solution of sodium selenite, especially on warming. Citric, tartaric, malic, and oxalic acids do not reduce sodium selenite in the cold, but do reduce strong solutions of the selenite on boiling with a slight excess of the acid. Hydrochloric acid has no reducing action on the selenite solution. Citric, tartaric, malic, and oxalic acids have a reducing action likewise on ferric salts, converting them to the ferrous form. Unsaturated fatty acids such as oleic and elaidic also have the power to reduce sodium selenite and tellurite to metallic selenium and tellurium on warming the mixtures on the water bath. Dextrose likewise reduces the selenite and tellurite on warming. A strong solution of sodium selenite mixed with a solution of invert sugars made by warming cane sugar with dilute hydrochloric acid was completely reduced in the slightly acid mixture on standing 48–72 hours at the room temperature of about 30° C.

JONES (**29**) injected selenate into the blood of animals. The selenate was reduced to selenite, a small part of which was excreted in the urine. The remainder was carried to the spleen and liver, where it was reduced by dextrose to selenium. When the dextrose was exhausted, fat was called upon. JONES suggests that dextrose is possibly the means by which all reduction processes in the body are brought about. He found that arabinose, glucose, and sugars yielding glucose would reduce sodium selenite on heating, while levulose could reduce it at 30° C. on long standing.

As regards the reduction of sodium selenite and tellurite by wheat roots, it seems probable, since no reducing enzyme could be extracted from the crushed plant, although the juice did show reduc-

tion of selenite upon heating, that the reduction is due to the metabolic activities of the roots, to some unstable non-enzymotic bodies comparable to the oxyorganic acids, which have a slight reducing power, or to complex, unsaturated compounds comparable to dextrose and levulose or the unsaturated fatty acids.

In regard to the significance of the reducing power, it may be said that reduction in organisms runs in general concurrently with oxidation, and is probably just as important an index of life activity. A better medium than sodium selenite is required, however, for a detailed study of this reducing power. Such a medium would be a chromogen which changed color under the reducing action, and thus would present a possibility of estimating the change colorimetrically and quantitatively. The fact stands, however, that the growing root possesses reducing powers.

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STUDIES ON THE PHLOEM OF THE DICOTYLEDONS[1]

I. PHLOEM OF THE JUGLANDACEAE

ANSEL F. HEMENWAY

(WITH PLATE XIII)

During the past year the writer has studied the phloem of *Juglans nigra*, *Juglans cinerea*, *Carya ovata* (hickory nut), *Carya alba* (mocker nut), *Carya glabra* (pig nut), and *Pterocarya caucasica* (Caucausian walnut). The phloem of some thirty species of other lower dicotyledonous trees has also been investigated in a preliminary way. Next year this research will be continued. A general account of the literature on the subject will be presented in the subsequent paper.

The sieve tubes of the gymnosperms and the vascular cryptogams have sieve plates on their lateral walls as well as on their fusiform end walls; while in the angiosperms true and typical sieve plates are supposed to be confined to the oblique or horizontal end walls of the sieve tube. HILL[2] states:

> The term "sieve field," in the sense in which it is used in this paper, denotes the group of fine connecting threads or strings which are found normally on the lateral walls, and which serve as a means of communication between adjoining sieve tubes. The sieve plates occur on the horizontal or oblique end walls of the sieve tubes, and occasionally on the lateral walls also, but their slime strings are readily distinguished from sieve fields owing to their large size.

The object of the present research was to discover, if possible, any ancestral characters of the phloem, and especially to determine if the sieve tubes of any of the lower dicotyledons had lateral "sieve plates" instead of lateral "sieve fields."

In collecting material, it was found that the pieces of tissue from the main trunk of large trees were most satisfactory. Specimens taken from the trunk near the ground were texturally too

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 32.

[2] HILL, T. G., Histology of sieve tubes of the angiosperms. Annals of Botany 22:265. 1908.

irregular to be used for making radial sections. Phloem from large branches did not show much callus, specimens usually presenting in radial section but two or three rows of sieve tubes with callus.

The material used was cubes about a centimeter each way, which included the cambium as well as the phloem. These were killed, fixed, and softened, and then imbedded in celloidin. For general study the sections were double stained with hematoxylin-safranin and mounted in balsam. Russow's callus reagent was used to demonstrate the callus.

It will be appropriate to consider first the figures which accompany this paper. Figs. 1 and 2 show the topography of the phloem of *Carya alba* under lower power. The sections used for these were stained with hematoxylin-safranin. Fig. 3 is a higher-power magnification of a part of fig. 2. Figs. 4–6 are views of sections of *Carya glabra* that were recently treated with Russow's callus reagent.

Fig. 1 is a radial longitudinal section. At the left side of this section are seen two rows of sieve tubes with portions of end walls showing sieve plates in face view, and along the right side lateral sieve plates are shown in cross-section. The long, narrow, thick-walled cells are bast fibers. These usually occur in groups of three to six as seen in radial view.

The larger phloem parenchyma cells contain prismatic crystals which have elongated, nucleus-like spots in the center. The rays are made up of short parenchyma cells that have several simple pits where they come in contact with phloem parenchyma. A portion of a ray is shown in the left side of this section. No crystals have been observed in the ray parenchyma cells of any of the Juglandaceae studied.

Fig. 2 is a tangential section. Many crystal-bearing phloem parenchyma cells are seen in this view also. The large cells with oblique end walls are sieve tubes. They show the lateral sieve plates very strikingly in face view, and cross-sections of terminal sieve plates on the slanting end walls. This section shows but few bast fibers. The phloem parenchyma cells toward the lower right side of this figure, wherever their starch content is not too dark, may be seen to have densely pitted radial walls. The rays vary from uniseriate to multiseriate.

Fig. 3 is a high-power view of a part of that shown in fig. 2. On the left side there is again a good view of crystal-bearing phloem parenchyma cells. In the center there is a large sieve tube with lateral sieve plates covering the entire tangential wall. These lateral sieve plates when appropriately stained are found to be filled with angular pits with a fine netlike mesh between. They appear to be exactly the same as the terminal sieve plates.

Fig. 4 is a radial section of *Carya glabra*, stained with Russow's callus reagent. At the top and bottom are shown in face view terminal sieve plates covered with callus. Between these two sieve tubes are the dark spots of callus on the lateral sieve plates in cross-section.

Fig. 5 is a view similar to fig. 4. On the right is a portion of a ray showing the parenchyma cells with patches of dark-stained starch grains. On the left is again seen some phloem parenchyma cells containing large crystals.

Fig. 6 shows the center portion of fig. 5 more highly magnified. The dark dashes along the center are cross-sections of the deeply stained lateral callus. The writer has counted 40–50 of these in a straight line along the side of a large sieve tube.

Carya has relatively larger sieve tubes than *Juglans* or *Pterocarya*. In cross-section they are as much larger than the other elements of the tissue as medium sized vessels of the xylem are larger than the tracheids.

The phloem of *Juglans* and *Pterocarya* is much like that of *Carya*, but there are a few general characteristics by which they may be readily separated. The crystal-bearing phloem parenchyma cells of *Juglans cinerea* and *Juglans nigra* are nearly cubical, and each contains a druse, while those of *Carya* are longer than wide and contain prismatic crystals. *Juglans nigra* has very many crystals, especially in specimens from the trunk of large trees. Besides the crystals in the parenchyma, the bast fibers are often filled with rows of cubical crystals. These bast fibers of *Juglans nigra* occur in widely interrupted rings, while in *Juglans cinerea* the rings of bast fibers are nearly continuous. The bast fibers of *Juglans* and *Pterocarya* are thick-walled and keep a more or less circular outline; while *Carya* has relatively much more numerous

elements of the hard bast, yet as these are thinner-walled they tend to collapse and show an irregular outline in cross-sections.

The expanded ends of the large rays of *Juglans cinerea* are noticeable in rather thin specimens of phloem from young trees or small branches, but are seen in only rather thick phloem of *Juglans nigra*. The large sieve tubes of *Juglans nigra* and *Juglans cinerea* have long, crowded, lateral sieve plates like those shown in fig. 3 for *Carya*, but the smaller sieve tubes have sieve plates that are farther apart and have an oval or circular outline.

There are no crystals in the phloem of *Pterocarya* except druses in the parenchyma of root phloem. The phloem of *Pterocarya* has nearly continuous bands of bast fibers alternating with wider bands of sieve tubes and bast parenchyma. The lateral sieve plates in *Pterocarya* are practically the same as in *Juglans*, except that in the larger sieve tubes some of the longer sieve plates are divided obliquely by thin bars. The lateral sieve plates of *Juglans* and *Pterocarya* show equally as well developed callus as *Carya glabra*, though the sieve tubes do not appear to function as long. In some specimens taken from branches of *Pterocarya* and *Juglans*, callus was evident only on the fifth or sixth row of sieve tubes from the cambium. While in similar specimens of *Carya*, callus was present farther from the cambium and was on several rows of sieve tubes.

Where sieve plates occur on the side of a sieve tube next the companion cell, unilateral callus was observed. This callus resembles the unilateral callus described by STRASBURGER[3] on the sieve plates of sieve tubes of Abietineae next to the marginal ray cells.

Lateral callus is plentiful in the sieve tubes of *Castanea*, *Salix fragilis*, and *Populus trichocarpa*, though usually not so thick as on the end walls.

A sort of tyloses occurs occasionally in the older sieve tubes of the Juglandaceae. It is formed not by the wall of a parenchyma cell pushing in through a pit, as in the vessels of the xylem, but by a portion of the sieve tube wall subtending a parenchyma cell growing bodily into the sieve tube. The tyloses of the sieve tubes

[3] STRASBURGER, ED., Histologische Beiträge **3**:1891.

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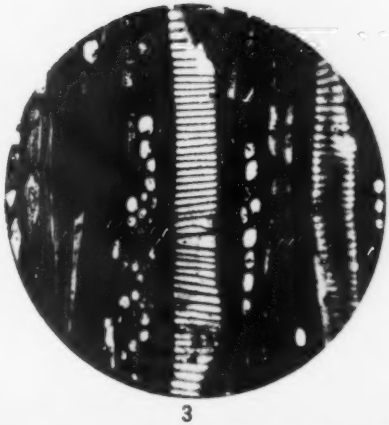

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HEMENWAY on JUGLANDACEAE

consequently resemble those occurring in the resin canals of certain conifers, rather than those found in the vessels of the angiosperms.

Summary

The six species of the Juglandaceae which have been considered possess well developed lateral sieve plates which have the same structure and appearance and seem to function in the same manner as the sieve plates on the end walls. The callus on the lateral sieve plates is identical in character with that on the end walls. The large sieve tubes have lateral sieve plates which are as crowded and as large as the terminal ones. This is contrary to the accepted views in regard to the sieve tubes of the dicotyledons. It would seem that we have here to do with an ancestral character, which indicates that the lower dicotyledons, as exemplified in the Juglandaceae, are more nearly related to the gymnosperms or vascular cryptogams. It is hoped that a further study of the phloem of the dictoyledons may disclose other ancestral traits, or aid somewhat in a systematic classification from an anatomical standpoint.

This work has been done in the Phanerogamic Laboratories of Harvard University under the direction of Professor E. C. JEFFREY, to whom the writer wishes to express his thanks for assistance and helpful advice.

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EXPLANATION OF PLATE XIII

FIG. 1.—*Carya alba:* radial longitudinal section of phloem. ×40.

FIG. 2.—The same: tangential section of phloem. ×40.

FIG. 3.—A higher-power view of part of what is shown in fig. 2. ×180.

FIG. 4.—*Carya glabra:* radial section stained to show callus on the sieve plates of the sieve tubes. ×180.

FIG. 5.—The same: a similar view of the radial section. ×180.

FIG. 6.—The same: showing a central portion of fig. 5 more highly magnified. ×500.

OENOTHERA LAMARCKIANA: ITS EARLY CULTIVATION AND DESCRIPTION

E. J. Hill

The question raised by Dr. R. R. Gates in a recent number of *Science* (N.S. **31**:425. 1910) as to the earliest description and origin of *Oenothera Lamarckiana* Seringe, the importance of which is expressed in a notice in the Botanical Gazette (**50**:79. 1910), is the occasion of some historical investigation I have made along the same lines. Gates takes as the earliest description one in manuscript in the form of a long marginal note in a copy of C. Bauhin's *Pinax*, forming one of the Sturtevant collection in the library of the Missouri Botanical Garden. It was apparently written by one Joannis Snippendale, and is considered as written from the living specimens. In the *Pinax* the plant is called *Lysimachia lutea corniculata*.

Gates gives four characteristics to show that the description applies to a plant of *O. Lamarckiana* and not to *O. biennis* L. or to *O. grandiflora* Ait. These are in the main the form of the rosette leaves, the large flowers, the type of hair arising from reddened papillae, and the quadrangular buds. But taking these as the criteria, I fail to see in what respect it is not essentially the same as a lengthy description made by Bauhin and published in 1623 in the appendix to the *Pinax* (pp. 520, 521). This of necessity is older than any marginal one placed in a copy subsequent to publication, with the additional advantage of a definite date, if applicable to the same species. The *Pinax* is mainly a bibliography of botany, up to the time of its publication notes or brief characterizations being frequently added to the various topics. In the appendix are corrections of errors made in some of the earlier printed parts, an interruption in the printing affording an opportunity for this, and for the addition of other matter. These are mostly descriptions of plants mentioned in the body of the book, or of new forms, all longer than those customarily given. The longest and fullest of these is *Lysimachia lutea corniculata*, mentioned in the previous

part of the work (p. 245), where but five lines were devoted to it, here fifty-three, or more than a column of the double-columned quarto. It has every appearance of being based on the living specimens growing in his garden. Near the close of the account he says:

> We received the seed of this [plant], under the name of *Lysimachia virginiana*, from Padua in 1619. Being sown in the spring it remained all summer and winter without a stem, but in the following year produced a stem towards the end of spring and began to flower in June. From the seed, which falls in autumn (for the plant is annual), it blooms abundantly in my garden every year, even up to the close of autumn.

The phraseology on p. 245 is slightly different, and is the one I usually see quoted. Under *Lysimachia lutea corniculata* it is stated:

> The seed itself, which was sent from Padua in 1619, grew finely in the garden, and it is readily spontaneous from the fallen seed up to this time.

The account in the appendix may not be in all copies. A second edition of the *Pinax* was published, in references to which I find different dates attached (1661, 1675). On a flyleaf of my copy is written by some unknown hand "Une 2^{me} Edition sans changement parût en 1671." It was a reprint. Authors sometimes cite one of these references, sometimes both, but that on page 245 when but one is given. Thus GRONOVIUS in CLAYTON'S *Flora virginica* (p. 58, 1762), under *Lysimachia lutea corniculata*, gives only p. 245. LINNAEUS, in his *Hortus Cliffortianus* (p. 144, 1737), gives both, but has p. 516 instead of 520, perhaps a typographical error; if not, it shows discrepancies in copies. Much of the description which covers this and other references to *Lysimachia lutea* by various authors cited in RAY'S *Historia plantarum* is a verbatim transcript of BAUHIN'S in the appendix to the *Pinax* (1:862. 1686). There are some omissions and a few minor changes and additions. But these might be needful, as he sought to include variations or forms covered by four descriptive or adjective terms (*virginiana*, *siliquosa*, *corniculata*, and *americana*) published between 1623 (BAUHIN) and 1651 (FABIUS COLUMNA).

The time of introduction of *O. Lamarckiana* into Europe is taken to be about 1614. LINNAEUS (*Hort. Cliff.*) says: "Brought

to Europe 120 years ago [1617 according to date of publication], now become spontaneous and growing everywhere in the sandy fields of Holland." A. DE CANDOLLE (*Géographie Botanique* 2:711. 1855) cites this passage from LINNAEUS, and an additional one from his *Species plantarum* (2d edition): "Hab. in Virginia, unde 1614." This last date is given by LAMARCK and MIRBEL in their *Histoire naturelle des végétaux* (13:82. 1803):

> Cette plante originaire de la Virginie et du Canada, a été apportée en Europe en 1614; elle s'y est tellement multiplicée qu'on peut la regarder comme naturalisée.

This is of course under the Linnean species *O. biennis*.

But one of the most important passages leading up to the introduction of the plant, and throwing light on its early history, is in the work of DE CANDOLLE just mentioned. He devotes considerable space to the naturalization of plants and the approximate time of introduction into different countries and their most probable place of origin. In his article *Naturalisation à grande distance*, *Oenothera biennis* L. has a prominent place. This includes the different forms segregated by others. After giving the passage quoted above from BAUHIN'S *Pinax* (p. 245), but with no allusion to the corresponding one in the appendix or mention of the description there, he says (2:711):

> Mon père a vu dans l'herbier de BAUHIN à Bâsle l'échantillon authentique venant d'un jardin, et il a vérifié que c'est bien l'*Oenothera biennis* L. actuellement répandu dans plusieurs parties de l'Europe. L'édition du *Pinax* de 1661 ne dit rien de plus que la première. JEAN BAUHIN n'en parle pas. P. ALPINUS (*Exot. ann.* 1627, p. 325) donne une figure où l'on reconnait l'espèce; il la nomme *Hyoscyamus virginianus*, et il dit: "Ab hinc annos duos mihi nata est planta ex seminibus nomine *Lysimachiae virginianae* ad me missis a JOANNE MORO medico et philosopho anglo erudissimo." Peut-être cette phrase a-t-elle été écrite quelques années avant la publication de l'ouvrage, par exemple vers 1621 ou 1622, de sorte que la culture dans le jardin de Padoue, dont parle PROSPER ALPINUS, serait la même dont C. BAUHIN faisait mention. Quoi qu'il en soit, il me parait évident que l'*Oenothera biennis* était alors cultivé dans le jardin de Padoue, comme une plante rare.

The attempt to reconcile dates made in this passage by DE CANDOLLE is readily obviated. He does not seem to recall that ALPINUS died in 1617, and that the work from which he quotes was a post-

humous publication by his son (*De plantis exoticis libri duo.* Venice. 1627), so that he could not have written this in 1621 or 1622, nor sent seeds to BAUHIN in 1619. Born near Venice, ALPINUS became professor of botany in the University of Padua in 1593, and, if not then, somewhere between that time and 1617, the date of his death,[1] became director (*praefectus*) of the botanic garden at Padua.

Though BAUHIN could not have obtained the seed from ALPINUS in 1619, we are not devoid of a clue to the garden at Padua. Fortunately, among other sources for his *Pinax* which BAUHIN gives, is a preliminary page with the heading *Nomina eorum qui plantas vel semina communicarunt.* Three of these were connected with the garden at Padua. The dates are not given, but the order of succession places them: (1) "JACOBUS ANTONIUS CORTUSUS, quintus Patavini horti praefectus"; (2) "PROSPER ALPINUS, Profess. et horti Patavini sextus praefectus"; (3) "JOAN. PREVORTIUS, Med. Professor et horti Patavini septimus praefectus." The succession being without a break, and the time being so short between the death of ALPINUS and the reception of the seed by BAUHIN in 1619, taken in connection with his full and careful record of sources, leaves little room for doubt that they were obtained from PREVORTIUS, the seventh director of the garden.

There is, however, a very narrow interval between the commonly accepted date of introduction from America and the death of ALPINUS (1617), in which he states that he raised plants from seeds obtained from Dr. MORE. For the "two years ago" ("ob hinc duos annos") refers evidently to the time when the plants came up and not to the date of reception. Two years had elapsed between the appearance of the plants and the writing of the account. It would be necessary to place the date of introduction as early as 1614 at least. The figure of the plant in the work of ALPINUS, therefore, must be a representation of one almost at the beginning of its appearance in Europe. DE CANDOLLE, comparing the figures of *Lysimachia lutea siliquosa virginiana* given by PARKINSON in his earliest work (*Paradisus*, 1629) and in his second work (*Theat-*

[1] BAILLON, Dict. de Botanique. Art. PROSPERO ALPINI; SPRENGEL, Gesch. der Bot. 1:356. 1817.

rum, 1640) with that in ALPINUS (*Exot.*, 1627), says that the petals differ, being strongly mucronate in the *Theatrum*, lightly so in the *Paradisus*, emarginate as in the modern plant in ALPINUS, and that PARKINSON'S plant is perhaps different (p. 712). I have seen that in the *Paradisus* (the reprint, London, 1904) and can confirm the statement as to this. The mucro is so broad and low in some of the petals as to give the tips a wavy appearance. The plant is a little branched, and it is stated that it may reach the height of a man. BAUHIN gives this height also. With regard to the form of the petals, DE VRIES mentions a similar discrepancy between the description by LAMARCK of *O. longiflora* Jacq., and the specimen from LAMARCK found in the herbarium of the Museum d'histoire naturelle at Paris. The description says they were rounded, the example shows that they were obcordate.[2] All tends to show that differences, specific or not, existed in the cultivated plants at so early date that they must have been present in a wild state in America before the introduction into the gardens of Europe.

By whatever means the plants may have reached Europe, we may conclude that the line of transmission of what is now recognized as *O. Lamarckiana* up to the time of the publication of BAUHIN'S description in 1623 was as follows: from JOANNES MORUS of England to PROSPER ALPINUS at Padua, 1614 or earlier; from JOANNES PREVORTIUS of Padua to C. BAUHIN at Bâsle, 1619. His description may therefore be pretty safely dated within nine years or less of the probable introduction.

CHICAGO

[2] DE VRIES, HUGO, Die Mutationstheorie 1:316, 317. 1901.

BRIEFER ARTICLES

MELCHIOR TREUB

(WITH PORTRAIT)

Dr. MELCHIOR TREUB was born at Voorschoten, near Leiden, December 26, 1851, and died at Saint Raphael, near Cannes, October 3, 1910. From 1869 to 1880 he was at the University of Leiden, first as a student and then as an instructor. In 1880 he was appointed Director of the Botanic Garden at Buitenzorg, Java, to succeed Dr. SCHEFFER.

It was in this directorship of nearly thirty years that TREUB displayed that power of organization and of administration, coupled with the spirit of research, which so distinguished him. He found the garden a scientific institution, but he discovered that increased opportunities for scientific work could be secured most readily through cooperation with agricultural interests. Upon this basis he secured private gifts in addition to grants from the government, and under his wise management Buitenzorg became the conspicuous center of research related to tropical agriculture, as well as the best equipped tropical station for purely scientific investigation.

The provisions for visiting botanists are exceedingly generous, the whole atmosphere of the institution suggesting that this is its chief purpose. Not only is there an especially well equipped "visitors' laboratory," but reagents and native collectors are freely supplied. As a result of this liberal policy, combined with the wide range of tropical conditions, the list of visiting botanists is very impressive, both in number and standing.

The *Annals* published by the Garden was established by Dr. SCHEF-

FER, but its editorial management came to TREUB with the second volume. This has been the natural medium of publication for the scientific work of the Garden, and its files represent well the nature and importance of this work. TREUB's own contributions were exceedingly varied, not being guided so much by any special phase of botany as by the opportunity presented by the tropics. Hence they are cited in the literature of morphology, of physiology, and of ecology; and all of them are characterized by clear insight and fine presentation.

His resignation in 1909 was compelled by ill health, brought about in connection with the work of enlarging the scope of the Garden by making it a part of a Department of Agriculture in Java. He intended to live in the Riviera and to prosecute his own studies, but he was forced to spend the winter in Egypt, and did not reach Saint Raphael until spring. It was a great gratification to him that he lived to see the publication of the *Festschrift* in his honor, to which about sixty of his scientific colleagues contributed.—J. M. C.

DAVID PEARCE PENHALLOW

(WITH PORTRAIT)

By the death of Professor D. P. PENHALLOW of McGill University, Montreal, at the untimely age of fifty-six, American Botany has lost a pioneer and leader in his particular field. Born at Kittery Point, Maine, he traveled widely, giving his attention at various times to many different activities. One of the founders and for a time the acting president of the Royal Agricultural College, Sapporo, Japan, he manifested after his return from that country an enthusiastic admiration and even love of the Japanese. Domiciled later for over a quarter of a century in the Dominion of Canada, he became, without losing his American affiliations, so much a part of the academic family of McGill University, that he was, for a number of years one of its Governors. It seems probable that the attempt to carry on his scientific work and at the same time to do his share of the numerous administrative duties which fell to his lot in the country of his adoption, was the primary cause of his early decease.

PENHALLOW's earlier work in his chosen science was on the ascent of sap in wood, and this initial inclination seems to have dominated more or less his whole life. After gaining his degree at Amherst, he set out at an early age for Japan, where he rendered valuable services in connection with the awakening of the scientific activities of that remarkable nation. During his stay in Japan, he visited the Aino in the

northern island and was the first person of western origin to live among them. He collected many data and made many photographs illustrative of his observations among these people, which have unfortunately never been published. His sojourn in Japan, however, had one important result, namely that of directing the attention of the young scientist to the extremely interesting arboreal flora of these islands. After his return to the United States, in 1880, he spent several years in special investigations at Cambridge, Mass. When Sir WILLIAM DAWSON of McGill University called upon ASA GRAY to send him a young man qualified to initiate botanical studies, PENHALLOW was the choice. His relations with Sir WILLIAM DAWSON, a distinguished geologist and paleontologist, gave a paleobotanical bent to the scientific investigations of the young botanist. During his earlier years at McGill, he published a number of articles on fossil plants, some of which were in collaboration with Sir WILLIAM DAWSON. Most important among these are his investigations on the gigantic Devonian seaweeds of Gaspé, Canada, and of another problematic vegetation from the Devonian of Kentucky, including remains of what must now probably be regarded as the earliest fernlike seed plants.

PENHALLOW early saw the need of the structural study of fossil plants, and in his later life was among the most prominent American authorities on the organization of extinct conifers. He gave his special attention to this field for nearly 25 years, publishing, in the early nineties, a key to the identification of coniferous woods, based upon their microscopic structure. The principles laid down by GOEPPERT, KRAUS, and other European masters in this field were used for the elucidation of the structure and affinities of American conifers living and extinct. Professor PENHALLOW was among the very first to attempt to interpret the evolutionary sequence of the conifers in terms of their

internal structure, thus providing a very fruitful and much needed control of the results reached along conventional systematic lines, from the consideration of the superficial characters alone. The early memoir of the *Anatomy of the conifers*, published in the *Transactions* of the Royal Society of Canada, appeared in 1907 in enlarged form as a book. Professor PENHALLOW was among the first to point out the remarkably isolated position of the araucarian conifers, which survive at the present day only in the southern hemisphere.

In those differences of opinion and interpretation which always prevail where scientific investigation is actively carried on, Professor PENHALLOW was a fair-minded and generous opponent. Whatever may be the fate of the particular hypotheses which he advocated, time cannot rob him of the credit of having realized the absolute necessity of attacking the Coniferales from the anatomical side, that is from within. His was a busy life, and within its short span he published articles amounting to upward of 200 titles. His industry and admirable personal qualities were fully appreciated by his scientific colleagues in the United States and Canada. For a number of years he was president of the Natural History Society of Montreal, and was likewise an important influence in the Canadian national scientific organization, the Royal Society of Canada. Nor was he overlooked in his native country. The presidency of the Society of Plant Morphology and Physiology, of the American Society of Naturalists, and of the Botanical section of the American Association for the Advancement of Science bestowed upon him made clear the appreciation of his fellows.—E. C. JEFFREY, *Cambridge, Mass.*

CURRENT LITERATURE

BOOK REVIEWS

The botanical system

In a recent published work,[1] TSCHULOK has sought to give a historical account of the development of the conception of the field of biology, principally botany, and of the logical delimitation of its parts. The historical résumé shows that before SCHLEIDEN (1843) botany had been expanding in ever widening circles of interest until it included the beginnings of almost all the present phases of the subject. The reform movement of SCHLEIDEN swept away all divisions excepting morphology and physiology, with taxonomy occupying an insecure position. This precedent has been followed almost universally, as may be seen by reference to the common general textbooks, such as the Bonn textbook. Ecology, plant geography, paleobotany, etc., are now demanding readmittance to the fold upon equal terms.

TSCHULOK enters into an exhaustive criticism of the several modern systems which have been proposed, and finds that none of them rest upon a logical basis. He then proposes a threefold division. From the standpoint of formal logic, botany is divided into biophysics and biotaxis, the former dealing with "real" relations and the latter with "ideal" relations; from the standpoint of instruction, it may be considered as either general or special; and lastly, there are "seven material viewpoints": (1) taxonomy, (2) morphology, (3) physiology, (4) ecology, (5) chorology, (6) chronology, (7) genetics. It is contended that these divisions include the whole field, and that nothing less will do so. An extended critique justifies this partition of the province of botany, and weighs the claims of such other subjects as pathology and economic botany. It is considered that economic botany, for instance, can have no place as an independent discipline, because in method and material it is in no way to be distinguished from these seven divisions, but rather it is part and parcel of each of them.

The consequences of circumscribing the field of botany, as is commonly done in "general" texts, is given full prominence. A single illustration will suffice. For a half-century paleobotany has been out of the texts and out of the usual courses of instruction. It has also been out of the minds of students, and those who might have taken up research in this field have been guided into other sorts of activity merely because of a lack of opportunity for a general outlook over the whole field of botany. As a result, the examination of this very important material has been left almost wholly to geologists who are usually quite untrained in botany.

[1] TSCHULOK, PHIL. S., Das System der Biologie in Forschung und Lehre. pp. x +409. Jena: Gustav Fischer. 1910.

At the present time, when many relatively new branches of botany are demanding recognition as coordinate with the old, such a critique of the historical and logical background of the science is especially welcome.—W. L. EIKENBERRY.

American men of science

President JORDAN'S recently issued collection of biographical sketches[2] brings together in a single volume and in very pleasing form the personal history and prominent achievements of seventeen American scientific leaders. The sketches are in all instances by a friend, a colleague, or at least a *Fachmann* of the scientist treated, and as a result combine in high degree insight and sympathy. The selection of the seventeen scientists most worthy to be included in such a series must have offered some difficulty, though such appropriate names as AGASSIZ, AUDUBON, RUMFORD, GRAY, DANA, and some others will occur at once to the layman as well as to the scientific student. The distribution as to subject is not without interest. Of physicists there are four, and of zoologists three; while ornithology, paleontology, and geology have two each; and botany, chemistry, anatomy, and astronomy claim each a single representative.

The interest of the botanical reader will naturally center upon the account of Dr. GRAY, whose life and work are treated with obvious affection by his pupil and friend Professor JOHN M. COULTER. Sketching clearly what is known of Dr. GRAY'S early history, he brings out vividly as he proceeds the unity of purpose, unflagging diligence, extraordinary capacity, and grand achievements which characterized GRAY'S career. Finally, he is able from personal acquaintance to add many more intimate touches, which give life to the sketch and make the reader feel acquainted with the charming personality of its subject. As those capable of giving them decrease, these personal reminiscences of Dr. GRAY become the more precious.

In perusing the various biographies here assembled, one is impressed by the fact that GRAY more than any other of these men, if perhaps we except Count RUMFORD who lived in Europe, and AGASSIZ who was born and educated there, stood in the closest relation to European activities in his science and did much to correlate and harmonize the intellectual endeavors of the New World and the Old.

Without any lack of patriotism it may be pointed out to publishers that works on distinguished Americans are rendered no more attractive by much gilt or by a squashed eagle painfully recalling the unhappy bird on the demonetized trade dollar. However, notwithstanding its forbidding appearance, the volume furnishes fascinating reading and gives information and stimulus in no small measure. "There were giants in the earth in those days."—B. L. ROBINSON.

[2] Leading American men of science. Edited by DAVID STARR JORDAN. Illustrated. 8vo. pp. 471. New York: Henry Holt & Co. Forming one of a series of volumes, edited by W. P. TRENT, devoted to biographies of leading Americans.

NOTES FOR STUDENTS

Graft hybrids and chimeras.—The large amount of recent work on graft hybrids, which has resulted in such astonishing discoveries as to their exact nature, seems to call for a collective review. In 1825 M. ADAM, a French horticulturist, by grafting *Cytisus purpureus* (a small tufted species) on *Laburnum vulgare* (an arborescent species) was much surprised to find that there resulted a shoot with somewhat intermediate characters. While the original individual has long been dead, the new form has been propagated by grafting and is somewhat common in cultivation; to it there has been given the name *Laburnum Adami*, and generally it has been regarded as a graft hybrid. Scarcely second in reputation to this, the most famous of the "graft hybrids," is *Crataegomespilus*, which is supposed to be a graft hybrid between *Crataegus monogyna* and *Mespilus germanica;* in this case the original tree is said still to exist in Lorraine. A third supposed case of a graft hybrid is the Bizzaria orange, which is thought to have arisen through the intergrafting of *Citrus Aurantium* and *C. medica*. While much study has been made of these peculiar plant forms, it is only very recently that their nature has been understood.

The present phase of graft hybrid investigation dates from a paper by HANS WINKLER, published in 1907.[3] Although the results of this first paper were somewhat disappointing, they deserve mention, because they opened up a new method of investigation. A scion of *Solanum nigrum* was grafted on *S. Lycopersicum*, and after growth had been resumed, a transverse cut was made in such a way as to sever both stock and scion, it being hoped that adventive shoots would grow from the cut surface along the line of contact of stock and scion. Such adventive shoots actually appeared, and in one case the new shoot involved tissues of both stock and scion. However, the new form was not a graft hybrid, for clearly one side of the shoot was *Solanum nigrum* and the other *S. Lycopersicum;* to this peculiar structure WINKLER gave the suggestive name *chimera*. So sharply marked was the line between the tomato and the nightshade that some leaves were partly of one species and partly of the other. WINKLER'S method soon yielded the results he had been seeking, for in 1908 he announced the production of a true graft hybrid,[4] a notable result, since never before had this been done under exact experimental control. To the new form there was given the name *Solanum tubingense*, in honor of the university town where the plant was produced. Out of 268 grafts between the tomato and the nightshade, there arose over 3000 adventitious shoots, among which there were five chimeras and the supposed graft hybrid *Solanum tubingense;* the latter, while intermediate in character, is somewhat closer to the nightshade than to the tomato. Early in 1909 WINKLER reported

[3] WINKLER, HANS, Ueber Propfbastarde und pflanzliche Chimären. Ber. Deutsch. Bot. Gesell. **25**:568–576. *figs. 3.* 1907; see BOT. GAZETTE **47**:84. 1909.

[4] ———, *Solanum tubingense*, ein echter Propfbastard zwischen Tomate und Nachtschatten. Ber. Deutsch. Bot. Gesell. **26***a*:595–608. *figs. 2.* 1908; see BOT. GAZETTE **47**:250. 1909.

the production of several more "graft hybrids" by the use of the same methods.[5] In this paper four varieties of graft hybrids are described, and are given the names *Solanum Darwinianum*, *S. Gaertnerianum*, *S. proteus*, and *S. Koelreuterianum;* the first two resemble the nightshade more than the tomato, while the last two are closer to the tomato. Some of the new forms appeared more than once in the cultures, *S. Gaertnerianum*, for example, being observed to arise five times. Some of the new forms appeared as branches from chimeras. In a recent paper[6] WINKLER reports the results of a study of the progeny of the new forms. Although the vegetative shoots seem able to fuse and merge readily in various ways, the tomato and nightshade cannot be hybridized sexually. WINKLER observes that the "graft hybrids" without exception revert to the nearer parent, the seedlings of *Solanum tubingense*, *S. Darwinianum*, and *S. Gaertnerianum* always being *S. nigrum*, while the seedlings of *S. proteus* and *S. Koelreuterianum* always are *S. Lycopersicum*. The new forms may be hybridized sexually with the nearest parent form, the progeny being pure nightshade or tomato, as the case may be. Furthermore, reversion in the vegetative shoots is to the nearer parent form.

While WINKLER'S results are accepted without debate, his interpretation has been called in question by various investigators. It may be noted that the behavior of the new *Solanum* forms is altogether like that of *Laburnum Adami*, which often shows vegetative reversion to one of the parent forms, and whose seeds give rise not to *L. Adami*, but to *L. vulgare*. STRASBURGER, who always has consistently opposed the reality of graft hybrids on cytological grounds, has taken up the new *Solanum* forms, calling them *hyperchimeras*, that is, more or less complicated chimeras, in which the elements of the two parent forms are more or less intermingled but without any real nuclear fusion (see below).[7] Of much greater significance are some recent investigations by ERWIN BAUR, and his results bid fair not only to cause a different interpretation to be placed upon WINKLER'S results than has been made by either WINKLER or STRASBURGER, but to revolutionize our notions along certain lines as to the possibilities of plants. BAUR has found from a careful study of geraniums with white-margined leaves[8] that the green cells and colorless cells each are descended from others of their kind, the peripheral portions (composing two or three rows) being colorless (though containing chromatophores) and the internal portions green, and the limits between them being

[5] WINKLER, HANS, Weitere Mitteilungen über Propfbastarde. Zeitschr. Bot. **1**:315–345. *pl. 1. figs. 4.* 1909; see BOT. GAZETTE **48**:478. 1909.

[6] ———, Ueber die Nachkommenschaft der *Solanum*-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. Zeitschr. Bot. **2**:1–38. 1910; see BOT. GAZETTE **49**:386. 1910.

[7] STRASBURGER, EDUARD, Meine Stellungnahme zur Frage der Propfbastarde. Ber. Deutsch. Bot. Gesell. **27**:511–528. 1909.

[8] BAUR, ERWIN, Das Wesen und die Erblichkeitsverhältnisse der "Varietates albomarginatae Hort." von *Pelargonium zonale*. Zeit. Abst. Vererbungslehre **1**: 330–351. *figs. 20.* 1909; see BOT. GAZETTE **48**:72. 1909.

sharp. Since the sexual cells are from the peripheral white portion, the seedlings give pure white forms. White branches give only white forms vegetatively, and green branches only green forms. If a pure white and a pure green form are hybridized sexually, there result, besides pure white and pure green offspring, green-white mosaics. If in the latter the growing point is situated on the line between the white and green portions, there results a chimera, such as WINKLER obtained so frequently in *Solanum*. Since in a cross-section of a stem the two components appear as sectors, BAUR has given to such forms the name *sectorial chimeras*. For the condition that BAUR finds in an ordinary *Pelargonium* with white-margined leaves, he gives the name *periclinal chimeras*, one of the components investing the other; in *Pelargonium* the growing point is periclinally divided into white and green cells, the former outermost, so that the entire plant is composed of a body of green geranium invested by a mantle, two or three cells deep, of white geranium. In referring to WINKLER'S work, BAUR suggested that the so-called graft hybrids of *Solanum* probably are periclinal chimeras. In another paper[9] he discusses STRASBURGER'S theories concerning hyperchimeras, noting that such an irregular mixture of the elements of the two component forms can hardly give rise to such definite structures as the so-called graft hybrids. Very recently BAUR has published a résumé of his work on *Pelargonium*, and on the graft hybrid question generally.[10] He has discovered also that *Crataegomespilus* is a periclinal chimera, the form known as *C. Asnieresii* being composed of a *Crataegus* body with a *Mespilus* epidermis; while the form known as *C. Dardari* has a *Mespilus* periphery of two cell layers. *Laburnum Adami*, which has been a riddle for nearly a century, proves to be a periclinal chimera, with an epidermis of *Cytisus purpureus* and a body of *Laburnum vulgare;* seedlings are always the latter, because the hypodermal layer, which gives rise to the sex cells, is of that species. When the peripheral species is composed of two or more layers, the seedlings are of that species, as in *Pelargonium*. One of the most interesting features of a situation that is throughout of absorbing interest is that BAUR'S remarkable discovery was almost made by MACFARLANE[11] fifteen years ago, as BAUR himself points out. MACFARLANE made a careful anatomical study of *Laburnum Adami* in comparison with *Cytisus purpureus* and *Laburnum vulgare*, and an examination of his figures shows clearly that *Laburnum Adami* agrees with *Cytisus purpureus* as to its epidermis, and with *Laburnum vulgare* as to its body. Indeed MACFARLANE says: "The very striking resemblance which the epidermis of the hybrid portion has to that of *C. purpureus* . . . . would seem at first sight to prove that

[9] BAUR, ERWIN, Propfbastarde, Periklinalchimären, und Hyperchimären. Ber. Deutsch. Bot. Gesell. **27**:603–605. 1910.

[10] ———, Propfbastarde. Biol. Centralbl. **30**:497–514. *figs.* 7. 1910.

[11] MACFARLANE, J. M., A comparison of the minute structure of plant hybrids with that of their parents, and its bearing on biological problems. Trans. Roy. Soc. Edinburgh **37**:203–286. 1895.

the hybrid portion was wrapped around, so to speak, by an epidermis of *C. purpureus*." Very recently BUDER has reinvestigated *Laburnum Adami*,[12] and has brought additional evidence to show that BAUR'S view is correct. Finally, WINKLER, in his latest paper,[13] states that a study of his *Solanum* forms from BAUR'S viewpoint discloses that for the most part they are, as BAUR thought likely, periclinal chimeras. Here he suggests that what have been taken to be graft hybrids may (theoretically) be actual graft hybrids, resulting from the fusion of the somatic cells of different species; or again they may have a hybrid nature, owing to the migration between stock and scion of various substances (as atropin or nicotin in the Solanaceae); or finally they may be chimeras, where the possibility lies open that they may be hyperchimeras, sectorial chimeras, or periclinal chimeras. Careful cytological study has shown that *Solanum tubingense*, *S. proteus*, *S. Koelreuterianum*, and *S. Gaertnerianum* are periclinal chimeras. *S. tubingense* has a nightshade body and a tomato epidermis; *S. Koelreuterianum* has the reverse relation of the two components; *S. proteus* has a tomato periphery of two cell layers, and it is probable that *S. Gaertnerianum* has the reverse relation. WINKLER thinks, however, and the cytological evidence noted is confirmatory, that in *Solanum Darwinianum* he has a true graft hybrid that was produced by the fusion of vegetative cells of the nightshade and tomato. If this is proven to be correct, it will stand, not only as the first experimentally produced graft hybrid, but as the only certain instance on record of such a form. The discoveries of WINKLER and BAUR open a new path in experimental biology, and to one as much as to the other belongs the credit that goes to the pioneer; to WINKLER, because his brilliant work has made possible the experimental study of these problems, and because his studies mark the opening of a new line of investigation; to BAUR, because he has solved the riddle of nearly a century, and because he has made possible the interpretation of WINKLER'S results. It goes without saying that biologists will wait with eager expectancy the announcement of new results, and that many experimenters will be attracted to the new field.—HENRY C. COWLES.

The cytological aspect of graft hybrids and chimeras may be summarized as follows:

In 1905 and 1907, in papers dealing with the rôle of the chromosome in heredity, STRASBURGER[14] included an account of his investigations upon

[12] BUDER, JOHANNES, Studien an *Laburnum Adami*. Ber. Deutsch. Bot. Gesell. **28**:188–192. 1910.

[13] WINKLER, HANS, Ueber das Wesen der Propfbastarde. Ber. Deutsch. Bot. Gesell. **28**:116–118. 1910.

[14] STRASBURGER, E., Histologische Beiträge zur Vererbungsfrage. I. Typische und allotypische Kernteiluug. Jahrb. Wiss. Bot. **42**:1–70. *pl. 1*. 1905.

———, Ueber die Individualität der Chromosomen und die Propfhybriden-Frage. *Op. cit.* **44**:482–555. *pls. 5–8*. 1907.

Laburnum Adami. If this plant is really a hybrid, owing its origin to a fusion of diploid nuclei of *Laburnum vulgare* and *Cytisus purpureus*, its nuclei should be tetraploid; but they were found to be only diploid, and STRASBURGER regarded this as evidence against the hybrid character of the graft. After NĚMEC[15] had reported vegetative fusions of nuclei followed by reduction phenomena in chloralized root tips, STRASBURGER repeated the experiments, but could not confirm NĚMEC's results, and therefore concluded that they had no significance so far as *Laburnum Adami* was concerned, and also that in the structure of their nuclei, plants known as graft hybrids show no indication of a hybrid character.

At this stage in the development of the subject, WINKLER[16] secured from *Solanum Lycopersicum* and *S. nigrum* plants which were acknowledged to be graft hybrids, and he asserted that they would necessitate a fundamental revision of our theories in regard to inheritance, and especially in regard to the rôle of the nucleus in heredity. Since the threatened theories were due to STRASBURGER more than to any other botanist, he felt called upon to defend them, and securing material by grafting *Solanum Lycopersicum* and *S. nigrum*, he examined the nuclei, but did not find them to be different from those of other graft hybrids which he had previously investigated. There was no migration of nuclei, no fusion of nuclei of scion and stock, or any regulative reduction processes. He would regard WINKLER's graft hybrids as more or less complicated chimeras and would call them "hyperchimeras."

In many angiosperm parasites (like mistletoe) the relation between parasite and host is very intimate, but there is no mingling of nuclei. In grafting, it seems possible that a bud from the point of union might give rise to a shoot bearing a flower in which an anther might be from the scion and an ovary might be from the stock. Close fertilization might then give rise to a true hybrid, but hyperchimeras, STRASBURGER thinks, would be more likely to produce flowers, the seeds of which would give rise to pure plants of either the scion or stock.

The fact that pollen from his graft hybrids would cause fertilization in *Solanum nigrum* or *S. Lycopersicum*, while neither of these plants can be crossed with the other, WINKLER regards as proof of hybrid character; but STRASBURGER thinks that the pollen was probable pure, and consequently fertilizarion was to have been expected, but that only *S. nigrum* or *S. Lycopersicum* would result.

STRASBURGER publishes no figures and refrains from giving a detailed account of nuclear phenomena, because WINKLER's full paper has not yet been published; but his examination satisfies him that WINKLER has produced

[15] NĚMEC, B., Ueber die Entwickelung des Chloralhydrats auf die Kern- und Zellteilung. Jahrb. Wiss. Bot. **39**:645–730. 1904.

[16] WINKLER, HANS, Weitere Untersuchungen über Propfbastarde. Zeitschr. Bot. 1:315–345. *pl. 1. figs. 4.* 1909.

nothing which demands any fundamental revision of his theories in regard to the rôle of the nucleus in heredity.

Soon after this paper by STRASBURGER appeared, WINKLER[17] published a description of the generation obtained from the seed of his graft hybrids, and includes an account of the chromosome numbers. In *Solanum Lycopersicum* the x and $2x$ numbers are 12 and 24; while in *S. nigrum* they are 36 and (probably) 72. He suggests that the difference in chromosome numbers may prevent the crossing of these two species, although he recalls that ROSENBERG crossed two species of *Drosera* with 10 and 20 chromosomes in their x generation, and obtained a hybrid with 30 chromosomes as the $2x$ number. If the *Solanum* graft hybrids are due to a fusion of somatic nuclei, they should have 72+24, or 96 chromosomes, unless the fusion should be followed by a regulative reduction, in which case the number should be 48. WINKLER found the x number to be 36 in *Solanum tubingense*, *S. Darwinianum*, and *S. Gaertnerianum*, and found 12 in *S. proteus* and in *S. Koelreuterianum*, the first three of these, in their pollen formation, reverting to *S. nigrum*, and the other two reverting to *S. Lycopersicum*. The sterility of *S. Koelreuterianum* and *S. Darwinianum* might be due to a difference in chromosome numbers of microspores and megaspores. The microspore number is 12, but the megaspore number remains to be determined. In all five of the graft hybrids the development of the pollen is regular, but it is still to be determined whether the germ cells are pure or hybrid. WINKLER thinks it is more reasonable to suppose that the graft hybrids more closely resembling *S. nigrum* are from *S. nigrum* cells, and that those resembling *S. Lycopersicum* are from cells of that parent, the nuclei being those of one parent or the other, but the cytoplasm being mingled with that of neighboring cells. If such cytoplasm should have so great an influence, it would interfere with the theory that the nucleus is the sole bearer of hereditary characters.

In an addendum to this paper WINKLER severely criticizes STRASBURGER for publishing anything before the cytological details had been made public. STRASBURGER certainly would not have taken part in the matter had it not been that his cytological theories had been attacked. Had some cytological evidence accompanied WINKLER'S attack upon theories which STRASBURGER has held and defended almost for a lifetime, any unpleasantness could have been avoided. In this addendum WINKLER states that in September 1907, at the Dresden meeting of the *Deutsche botanische Gesellschaft*, he had suggested that the *Solanum* graft hybrids might be complicated chimeras, a sort of mosaic of the two parents. This suggestion seems to the reviewer to be a good working hypothesis, and if the suggestion is really a fact, an intensive study of the nuclei and cytoplasm of the graft might enable one to recognize, even in vegetative tissues, just what cells have been derived from each parent, while in the reduction divisions the recognition should not be difficult.

[17] WINKLER, HANS, Ueber die Nachkommenschaft der *Solanum*-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. Zeitschr. Bot. **2**:1–38. 1909.

That there is an interchange of material between nucleus and cytoplasm probably all cytologists will admit, although optical evidence is at present very scanty. It seems quite possible that the whole graft hybrid and chimera question, when the cytological evidence is all in, will emphasize rather than weaken the theory that the nucleus is practically the sole bearer of hereditary characters.

In his most recent account of the chromosomes of these forms WINKLER[18] finds that *Solanum tubingense*, *S. proteus*, *S. Koelreuterianum*, and *S. Gaertnerianum* are periclinal hybrids; while *S. Darwinianum*, at least in the subepidermal layer of the stem apex, is a fusion bybrid (*Verschmelzungs-Propfbastard*). The germ cells of this latter form have 48 chromosomes, and since the parents (*S. nigrum* and *S. Lycopersicum*) have 12 and 36 chromosomes as the reduced numbers, WINKLER infers that the subepidermal layer from which the pollen is derived must have 48 chromosomes; and he supposes that a *S. nigrum* cell with 24 chromosomes has fused with a *S. Lycopersicum* cell with 72, giving rise to a nucleus with 96; and that in the progeny of this nucleus the number has become reduced to 48. Another reduction would then give the required 24. This seems too complicated to be correct.

It is evident that cytological investigation of graft hybrids has only just begun. STRASBURGER early recognized the importance of such investigation, and WINKLER's splendid success in securing the grafts has reopened an attractive field for cytological research. The problems are so numerous and the time demanded for reliable results is so great that one man cannot hope to do all the work. Many have tried to find out whether there is a cytological basis for Mendelism. DEVRIES has welcomed cytological investigations of mutation and has generously furnished material for such work. If WINKLER should welcome others into the field, the facts might soon be uncovered; but if others must wait until he has finished, the task is so great and so complicated that, although a young man, he might grow old with the problem still unsolved. —CHARLES J. CHAMBERLAIN.

Plant diseases.—*Cyanospora albicedrae*, a new generic type, is reported on the mountain cedar of Texas by HEALD and WOLF.[19] The fungus is a pyrenomycete of a peculiar type, having its perithecia prostrate, with the short osteolum curved outward. The perithecia occur singly or in small groups on whitened areas on the trunks and branches. This whitening of the bark is the most characteristic symptom of the infected trees. The fungus is supposed to be a parasite, although its parasitism is not certain. The present paper is limited to a description of the fungus and its effect on the trees.

A new *Macrophoma* (*M. Phoradendri*) on *Phoradendron flavescens* (Pursh)

[18] WINKLER, HANS, Ueber das Wesen der Propfbastarde. (Vorläufige Mitteilung.) Ber. Deutsch. Bot. Gesell. **28**: 116–118. 1910.

[19] HEALD, F. D., and WOLF, F. A., The whitening of the mountain cedar, *Sabina sabinoides* (H. B. K.) Small. Mycologia **2**: 205–212. *pl. 31. figs. 3.* 1910.

Nutt. is described by WOLF[20] in the same journal. It infects the leaves, which it causes to fall.

An interesting organism belonging to the small group of parasitic slime molds (Phytomyxaceae) is described by SCHWARTZ[21] as occurring on the roots of some species of the Juncaceae. The organism belongs in the genus *Sorosphaera*, and in its development closely resembles the classic example of this group, *Plasmodiophora Brassicae* Woronin. In the earliest stages observed, the parasite consists of small multinucleate amoebae in the root hairs and outer cortical cells of the infected plants. The roots show no hypertrophy, and scarcely any other outward sign of the presence of the parasite, which can be discovered only by microscopic examination. In the vegetative stage all the nuclei of the amoebae divide simultaneously by the formation of a chromatic ring or plate surrounding an elongated karyosome. The process is identical with that described for *Plasmodiophora Brassicae*. At the beginning of spore-formation the protoplasm of the amoebae separates into a number of amoebulae, each with a single nucleus. The nuclei of the amoebulae undergo two divisions, forming four uninucleate spores. The spores remain loosely aggregated in sorospheres; their germination was not observed. The paper concludes with a brief description of *Entorhiza cypericola*, a member of the Ustilagineae inhabiting the roots of various species of *Juncus*.

BROOKS gives an account[22] of the development of *Gnomonia erythrostoma*, which causes the leaf-scorch disease of the sweet cherry. The mycelium, which is intercellular in the tissues of the leaves, consists of multinucleate cells, resembling in this respect other ascomycetes except the mildews. The first fruiting organs to appear are spermagonia, which are produced in great numbers on the lower surface of the leaves. The spermatia, which are discharged from the spermagonia in enormous numbers, are single-celled filamentous bodies with large nuclei and little cytoplasm. This structure, which BLACKMAN has pointed out as characteristic of male cells, leads the author to regard the spermatia as abortive male cells. The perithecia originate, as in other ascomycetes, as interwoven masses of hyphae near the lower epidermis. Branches from some of the outer cells of the mass protrude through the stomata of the leaf and bear a superficial resemblance to trichogynes. No case of their functioning as such was observed, however, although it often happens that a number of spermatia become attached to the protruding hyphae, a fact easily explicable when one considers the enormous number of spermatia produced. That the projecting hyphae do not function as trichogynes is further

[20] WOLF, F. A., A leaf blight on the American mistletoe, *Phoradendron flavescens* (Pursh) Nutt. Mycologia **2**:241–244. *pl. 32*. 1910.

[21] SCHWARTZ, E. J., Parasitic root diseases of the Juncaceae. Annals of Botany **24**:511–522. *pl. 40*. 1910.

[22] BROOKS, F. T., The development of *Gnomonia erythrostoma* Pers., the cherry leaf-scorch disease. Annals of Botany **24**:585–605. *pls. 48, 49*. 1910.

shown by the fact that they sometimes occur apart from any connection with the young ascocarps. Moreover, the development of asci proceeds in a region remote from the "trichogynes." The ascogonial hyphae are differentiated in the basal part of the mass of interwoven hyphae; they are characterized by their larger size and larger nuclei. No nuclear fusions were observed in the ascogonia, which seem to have lost their function and appear soon to degenerate. Apparently the ascogenous hyphae do not arise from them, but from other hyphae near the base of the perithecium, which appear after the ascogonia disintegrate. The asci arise from the terminal part of the ascogenous hyphae without the hook-formation common in ascomycetes. Other cells of the ascogenous hyphae may also grow out into asci. The ascus cells contain two nuclei which fuse as usual, whereupon three successive divisions occur, forming the eight spore-nuclei. The first of the three divisions is regarded as a reduction division, to counterbalance the single fusion which was observed. After the spore membrane has been formed, the nucleus of each spore divides again, a septum dividing the spore into two unequal cells being formed between the daughter nuclei.—H. HASSELBRING.

Insect galls.—The past few years have demonstrated an increasing interest in the study of cecidology, and, as in all biological subjects, the first work is taxonomic. A few of the interesting papers of the past few months are as follows: PEREZ[23] discusses the cecidia of *Eritrea*, describing 36 species of galls and one gall-maker. The descriptions are clear and the technical names of the host plants are given, but there are no figures. The VAN LEEUWEN-REIJNVAANS[24] discuss the cecidia of Java, describing 150 species on almost as many host plants. Most of these galls were collected at Salatiga at an elevation of about 600 meters; and they were found to be much more abundant in the moist than in the dry localities. Descriptions are given of the galls, and in many cases of the insects also, but the authors state that in describing the gall it is not necessary to describe the gall-maker, a view which is contrary to the views of some of our American entomologists, but with which the reviewer is in hearty sympathy. Most of the descriptions are accompanied by good figures. TROTTER[25] gives descriptions of 19 species of galls occurring on 14 host plants. His descriptions also include the bibliographies of those previously described. HOWARD[26] has described 52 species of Dr. SICHELS' collection, which is deposited in the Entomological Museum of Natural History in Paris. He also mentions a number of old galls of unknown origin. MASSALONGO[27]

[23] PEREZ, T. DE STEFANI, Altri Zoocecidii dell' *Eritrea*. Marcellia **8**:7–18. 1909.

[24] LEEUWEN-REIJNVAAN, J. und W., DOCTORS, Einige Gallen aus Java. *Op. cit.* **8**:21–35, 85*–122. 1909; **9**:37–61. 1910.

[25] TROTTER, A. Nuovi Zoocecidii della Flora Italiana. *Op. cit.* **8**:50–59. 1909.

[26] HOWARD, C., Les collections cécidologiques du Laboratoire d'Entomologie du Museum d'Histoire Naturelle de Paris: L'Herbier du Dr. SICHEL. *Op. cit.* 65–78.

[27] MASSALONGO, C., Galle e simili produzioni anormali. *Op. cit.* 133–141.

gives descriptions, with bibliography and in some cases figures, of 15 species. PANTANELLI[28] gives a lengthy description of a mite (*Eriophyes*) of the olive and also a description of its gall. RUBSAAMEN,[29] continuing his studies on the European cecidia, describes, and in many cases figures, 42 species, 4 of which are new. BAYER[30] in a paper on the cecidia of Bohemia gives a bibliography of 32 titles and lists 198 cecidia.

For a number of years the anatomy or rather the histology of cecidia has proved an interesting field for the European workers, but only in recent years has it attracted the attention of the American students. A recent paper is that of GREVILLIUS[31] on the anatomy of the thysanopterous cecidia of *Vicia Cracca*. This gall is very conspicuous because of the curling and twisting of the leaves which are infested with the insects, whose eggs can be found between the epidermis and mesophyll. In the more advanced stages the palisade cells lose their characteristic forms and become isodiametric. These galls never develop the complicated structures found in those produced by the hymenopterous insects.

Although the physiological problems connected with the study of insect galls have long been looked upon with interest, the difficulties have been so great that few have had the courage to attack them. One of the recent papers on this subject is by NALEPA,[32] who has taken up a study of the gall-inhabiting ants. This subject has been investigated by others, among them PEYRITSCH, who considered light the most important factor because there were more galls on plants growing under shade than in the light. NALEPA'S work took into consideration the relative importance of light, temperature, and moisture, and involved a number of experiments in which the insects were kept in cylinders, in which these factors could be controlled. In this connection he studied also other insects, such as *Eriophyes*, which he found were uninfluenced by the light. His results in general confirm the views of PEYRITSCH.—MEL T. COOK.

Transpiration.—RENNER[33] has published a paper on the physics of transpiration. It adds a number of important facts to the epoch-making work of BROWN and ESCOMBE on multiperforate septa. He works out mathematical formulae for the resistance to the passage of water vapor offered by stomatal apparatus of various xerophytes. The experimental part is carried out with models having the shape of xerophytic transpiratory canals and with plants

[28] PANTANELLI, E., Un Eriofide nuovo sull' olivo. *Op. cit.* 142–146.

[29] RUBSAAMEN, EU. H., Beiträge zur Kenntnis aussereuropäischer Zoocecidien. *l.c.* **9**:3–36. 1910.

[30] BAYER, EMILE, Les Zoocécidies de la Bohème. *Op. cit.* 63–104.

[31] GREVILLIUS, A. Y., Ein Thysanopterocecidium auf *Vicia Cracca* L. *Op. cit.* **8**:37–45. 1909.

[32] NALEPA, A., Der Heliotropismus der Gallmilben und seine biologische Bedeutung. *Op. cit.* 78–84.

[33] RENNER, O., Beiträge zur Physik der Transpiration. Flora **100**:451–547. 1910.

themselves. In agreement with BROWN and ESCOMBE, he states that loss of water vapor from leaves is through static diffusion, and that it is proportional to the differences of density of the vapor inside and outside the leaf. RENNER urges, as a thing of great importance, that the rate of diffusion will be inversely modified by an increase in the distance between the region of minimum density outside the leaf and the maximum density within the leaf. It is with methods by which this distance is modified that he is mainly interested. If the distance is great, the gradient is low and the flow is slow; if the distance is small, the gradient is high and the flow fast. One way in which this distance is increased in still air is by the water vapor cap which forms over the surface of the leaf. The larger the leaf, the greater the average thickness of the vapor cap. For this reason, in still air the amount of transpiration does not vary with the surface of the mature leaves, but is proportionally less for the larger leaves. RENNER believes that if the air were absolutely still it would vary as the diameter of the leaves.

Winds increase the transpiration of small mature leaves by a much greater percentage than it does the large ones. In wind the transpiration is proportional to the surface of the leaves. Again, the distance between the internal maximum vapor pressure and the external minimum may be increased by external or by substomatal cuticular cavities; if of the same size and shape, RENNER finds that the two have equal effects.

RENNER devised a means of experimentation by which he located the point of saturation within a rapidly transpiring leaf. He believes it often lies some distance from the stomata. In such cases a considerable system of intercellular spaces is involved in the diffusion. He emphasizes the fact that in such cases the stomata, if open, are only a small part of the diffusion canals, and therefore play a small part in the control of transpiration. In a similar way their importance as controlling factors is modified by internal and external cuticular chambers, and even by the vapor cap.—WILLIAM CROCKER.

Infection experiments with rusts.—In a preliminary report of some infection experiments made near Neuenburg (Switzerland), MÜHLENTHALER[34] shows that teleutospores of the *coronata* type of *Puccinia* from *Calamagrostis varia* produced aecidia on *Rhamnus alpina* and *R. Purshiana*. Aecidiospores from these reinfected *Calamagrostis varia* and *C. tenella* among several grasses tried. Aecidiospores collected on *R. cathartica* produced uredospores on *Bromus erectus* var. *condensatus*, *Festuca alpina*, *F. arundinacea*, *F. gigantea*, and *F. varia*. The uredospores thus produced on *Bromus erectus* var. *condensatus* could be transferred to *B. erectus* and its var. *condensatus*, *B. inermis*, *B. sterilis*, and *B. tectorum*.

In continuation of his cultural work on the Uredineae, ARTHUR[35] reports

[34] MÜHLENTHALER, F., Infektionsversuche mit Kronenrosten. Centralbl. Bakt. II. **26**:58. 1910.

[35] ARTHUR, J. C., Cultures of the Uredineae in 1909. Mycologia **2**:213–240. 1910.

the results of cultures of 1909, marking the beginning of the second decade of the work. In the season covered by the report, 15 species of rusts were each sown on a large number of aecidial hosts with negative results. Sowings of 23 species were made supplementing or confirming previous work of the author and others. Of special interest among these is the sowing of *Calyptospora columnaris* on potted plants of *Abies Fraseri*. The successful culture of the aecidia on *Abies* led to the subsequent discovery of the native aecidial form on *Abies balsamea* in Nova Scotia, whence the original *Calyptospora* material had been obtained. This collection of the aecidia by Professor FRASER is the first from America. Of teleutospore forms connected for the first time with aecidial forms, 6 are reported. These are *Puccinia Ceanothi* (Ellis and Kellerm.) Arth. on *Andropogon Hallii* Hack. and *Ceanothus americanus* L.; *Gymnosporangium exiguum* Kern on *Juniperus virginiana* L. and *Crataegus Pringlei* Sarg.; *G. corniculans* Kern on *J. horizontalis* Moench, *Amelanchier erecta*, and *A. canadensis* (L.) Medic.; and *G. trachysorum* Kern on *J. virginiana* L., *Crataegus punctata* Jacq., *C. coccinea* L., and *C. cerronis* A. Nels.—H. HASSELBRING.

Rate of photosynthesis.—THODAY[36] comes to the defense of the increased weight method of SACHS for determining the rate of carbon fixation in green plants. He thinks he has worked out the details of the method so as to insure quantitative accuracy. One cannot see how it will lead to more accurate results than the method described in GANONG'S *Plant physiology* (2d ed., pp. 92–97. 1908). In fact, it seems that THODAY'S experimental error must be greater than GANONG'S, due to the small leaf surface used. We know little about what occurs in a leaf subjected to illumination. As BROWN and ESCOMBE suggest in stating their CO_2 intake method, it may modify the power of various contained compounds to hold water at 100° C. Since the amount of atmospheric CO_2 fixed is the question to be answered, the reliability of the increased weight method must be measured by its agreement with the amount of CO_2 taken up under like conditions. It would seem as though the work better be done on perfecting the CO_2 intake method, if indeed BROWN and ESCOMBE did not leave it so. This method is entirely independent of asymmetry, of variation of surface with insolation, and of translocation and changes in the water-holding powers of the leaf. It also measures directly the thing sought. THODAY depended upon the horn hygroscope as a means of determining the condition of stomata. The results obtained with this instrument are at best only indirect and qualitative, as LLOYD[37] has suggested. The direct and accurate method devised by LLOYD is certainly preferable.—WILLIAM CROCKER.

[36] THODAY, D., Experimental researches on assimilation and respiration in the open air. Proc. Roy. Soc. London B **82**:421–450. 1910.

[37] LLOYD, F. E., Physiology of stomata. Publ. 82, Carnegie Institution. 1908.

Syndiploid nuclei.—In 1904 NĚMEC[38] showed that in vegetative tissues the nuclei of binucleate or multinucleate cells may fuse, giving rise to what STRASBURGER has called syndiploid nuclei and cells. In such cells the mitoses show a correspondingly high number of chromosomes, but in some cases the syndiploid condition disappears from the meristematic zone, and NĚMEC believed that a reduction of chromosomes had taken place. In a preliminary note[39] he mentions two kinds of reduction figures: one characterized by chromatin tetrads which split so that bivalent chromosomes arrive at the poles; in the other the diploid number appears suddenly without any tetrads, perhaps due to a fusion of chromosomes.

In chloralized roots tips of *Vicia Faba*, syndiploid cell rows are quite numerous in the lateral rootlets, but such rows often end blindly and are replaced by diploid rows. This may happen in different ways. A syndiploid row may be replaced directly by a diploid one, and in this case it is probable that a reduction of chromosomes has taken place; or the syndiploid initials may die and neighboring cells may crowd in; or peripheral syndiploid initials may cease to function. In these three ways it may come to pass that the lateral root may finally consist of only diploid cells.

It must be remembered that, while binucleate and multinucleate cells are rather common in plants, the syndiploid condition has as yet been studied almost exclusively in chloralized material.—CHARLES J. CHAMBERLAIN.

Sporogonium of Conocephalum.—Miss GRAHAM,[40] studying *Conocephalum conicum* (*Fegatella conica*), finds that at Ithaca, N.Y., the gametophores begin to appear in June, that fertilization takes place about the first of July, that the spores are fully formed before the beginning of winter, and that in the following May the gametophore stalk rapidly elongates. This elongation is quickly followed by the elongation of the stalk of the sporogonium. The venter of the archegonium is two-layered at the time of fertilization, and soon becomes a massive calyptra. The first division of the fusion nucleus gives rise to two free nuclei, which may lie parallel with or transversely to the major axis of the archegonium. A cell wall is not laid down until some little time has elapsed after division of the fusion nucleus; when the wall appears, it is transverse. By successive transverse divisions a filament of four or five cells is formed. This observation differs from that of CAVERS, who described an octant stage; the reviewer's observations agree with those of Miss GRAHAM. The first longitudinal walls appear in the outer or capsule end of the filament.

[38] NĚMEC, B., Ueber die Einwirkung des Chloralhydrats fau die Kern- und Zellteilung. Jahrb. Wiss. Bot. **39**:645–730. *figs. 157*. 1904.

[39] ———, Ueber das Schicksal der syndiploid Kerne und Zellen. Ber. Deutsch. Bot. Gesell. **29**:113–115. 1910.

[40] GRAHAM, MARGARET C., Development of the sporogonium and adjacent tissues of the gametophore of *Conocephalum conicum*. Bull. Torr. Bot. Club **36**:615–625. *pls. 30–33*. 1909.

At the time of separation of the mother cells, the growth of the capsule is checked, while the calyptra continues growth, leaving quite a space between capsule and calyptra. The capsule and seta soon resume growth, fill the cavity, and distend the calyptra. No pseudoperianth, such as is found in *Marchantia*, is present. A sheath, which is a specialized portion of the gametophore, invests the calyptra.—W. J. G. LAND.

Evaporation measurements.—The porous cup atmometer is now recognized by ecologists as one of the best instruments for measuring the evaporating power of the air, which is perhaps the most important climatic factor, or set of factors, in determining the vegetation of any locality. One difficulty in its operation has been that rain falling upon the exposed cup penetrates to some extent into the reservoir and vitiates the readings immediately following. To obviate this difficulty LIVINGSTON[41] has devised a rain-correcting atmometer with a mercury valve preventing any water from entering the reservoir. He also emphasizes[42] the importance of using nothing but the purest distilled water in the instrument and of standardizing the cups at frequent intervals. Recognizing the necessity of some uniform unit of standardization, in order that the results of the various workers may be comparable, he proposes that the standard cup be one that loses water at the same rate as 45 sq. cm. of water surface exposed in a Petri dish 1.5 cm. high and kept constantly filled to the depth of 3 mm. Microorganisms in the cups may be prevented by rinsing the cups and reservoirs with weak mercuric chlorid solution. It has also been found desirable to operate two or more cups at each station, as accidents are not likely to occur simultaneously to all, and thus an unbroken record is made more probable.—GEO. D. FULLER.

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[41] LIVINGSTON, B. E., A rain-correcting atmometer for ecological purposes. Plant World **13**:79–82. 1910.

[42] ———, Operation of the porous cup atmometer. Plant World **13**:111–119. 1910.

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